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Systematic Revision of Chinese Hipparion Species Described by Sefve, 1927

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ABSTRACT

Sefve's type series of Chinese Neogene hipparionine horses, in the Palaeontologiska Museet, Uppsala, is studied, along with relevant specimens housed by the American Museum of Natural History Frick Laboratories. Morphological and statistical analyses have been made of skull and directly associated mandibular material. The morphological analysis, using multiple states for 40 characters, identifies 11 hipparion groups in the assemblage. The statistical analysis documents range of variability in these morphological groupings and compares range of variability and size to the Höwenegg (late Miocene, Hegau, Germany) quarry sample. These analyses guide us in validating six of Sefve's (1927) original species: *Hipparion platyodus, Hipparion coelophyes, Hipparion hippidiodus, Hipparion ptychodus, Hipparion dermatorhinum,* and *Proboscidipparion sinense.* We follow Zhegallo's (1971) recommendation that Sefve's (1927) species *Hipparion richthofeni* be recognized as a taxon distinct from Koken's original material of *H. richthofeni* from Mongolia; we refer it here to "*H.*" *forstenae* (sensu Zhegallo, 1971). We recommend that four of Sefve's (1927) original taxa be considered nomina dubia: *Hipparion kreugeri, Hipparion plocodus, Hipparion tylodus,* and *Hipparion parvum.* The phylogenetic relationships of the valid species are discussed, and these species are found to represent parts of other known and some new lineages. The species "*Hipparion*" *platyodus,* "*Hipparion*" *coelophyes* (s.l.), and "*Hipparion*" *hippidiodus* are found to represent a morphoclinal series in China, but the coexistence of "*H.*" *coelophyes* (s.l.) and "*H.*" *hippidiodus* at the same localities and the later stratigraphic occurrence of "*H.*" *platyodus* provide evidence which rejects the hypothesis of their chronospecific relationship. "*Hipparion*" *platyodus,* "*Hipparion*" *ptychodus,* and *Proboscidipparion sinense* are cited as being potentially related to the "*Sivalhippus* Complex" which has a geographic distribution including mostly eastern and southern Asia and Africa. "*Hipparion*" *dermatorhinum* is believed potentially to be a monospe-

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cific lineage unique to northern Asia. "*Hipparion*" *forstenae* is found to be a member of the *Cremohipparion* lineage, which had a geographic distribution including China, western U.S.S.R., Greece, and Iran.

INTRODUCTION

Hipparionine horses have long been recognized as valuable index fossils for age discrimination of late Neogene Old World continental deposits. Recently there has been a renewed interest in this group, and a glance over the contemporary literature suffices to show how much progress has been made in understanding this group's evolutionary history. New discoveries have been made, especially as regards Old World early late Miocene forms (Vallesian age of European chronology). Many of the old museum collections from classical localities such as Samos, Pikermi, Maragheh, and the Siwalik Hills, Pakistan, have been restudied and revised (for a review see Bernor and Hussain, 1985; Bernor et al., in press; Woodburne, 1989). Since publications by Skinner and MacFadden (1977) and Woodburne and Bernor (1980), a number of the American paleontologists have become increasingly involved in formulating a superspecific classification of hipparionine horses. With the notable exception of work by Qiu et al. (1987), hipparionine research on Chinese assemblages has remained comparatively dormant. We believe that one of the principal reasons lies in difficulties of extending the existing nomenclature of the Uppsala type collection to other, newer Chinese discoveries.

Sefve's (1927) work is the first and only detailed description of the Uppsala hipparionine collection. Sefve described 44 skulls, some associated with lower jaws, and a number of isolated jaws and limb bones. Whereas the main portion of this assemblage was from Baode, there were some specimens from the Wuxiang-Yushe and Qingyang areas (see fig. 1 and table 1). Altogether Sefve (1927) described 11 new species and one new genus of hipparionine horses. While Sefve's work was a milestone in the systematic organization of the assemblage, it contains critical flaws. Sefve designated no type specimens, made no species diagnoses, paid little or no attention to ontogenetic variation (especially of cheek teeth), and entirely ignored the assemblage's geological age. No author has yet properly revised Sefve's (1927) initial work on the Uppsala assemblage. Because this collection is of key importance for all subsequent systematic work on Chinese hipparionines, and because there are accurate locality data associated with some of it, we believe that it is timely to revise the alpha systematics of the Uppsala collection and, building on the work by Qiu et al. (1987), to further develop hypotheses of these species' evolutionary relationships.

Three other major assemblages of Chinese hipparionines currently are housed at the American Museum of Natural History, New York; the Institute of Vertebrate Paleontology and Paleoanthropology, Beijing; and the Tianjin Museum, Tianjin. Currently, our joint project is to prepare and describe the American Museum Chinese hipparion collections. We provide here descriptions of those AMNH specimens that have recently been prepared, and are referable to species of the Uppsala type series.

Abbreviations and Definitions

Institutional

AMNH	Department of Vertebrate Paleontology, American Museum of Natural History, New York
F:AM	Frick fossil mammal collection, AMNH
IVPP	Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China
PMU	Palaeontologiska Museet, Uppsala, Sweden

Anatomical

MC III	metacarpal III
MT III	metatarsal III
POB	preorbital bar
POF	preorbital fossa

Hipparionine or hipparion—Any horse with an isolated protocone of the maxillary premolar and molar teeth, and, as far as known, tridactyl feet, including species of the following genera: *Hipparion, Neohipparion, Nannippus, Cormohipparion, Hippotherium,*

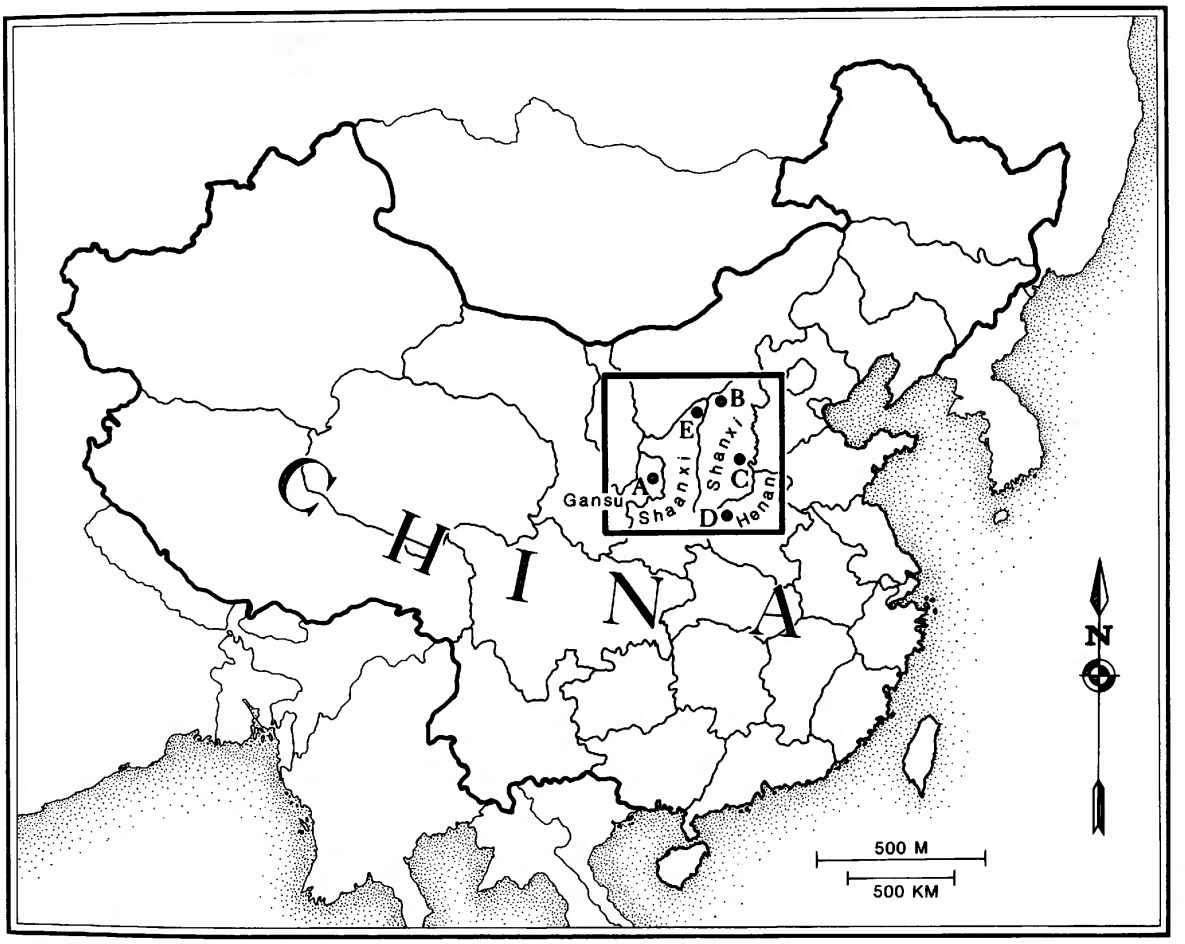

Fig. 1. Map of principal collecting areas of Uppsala Chinese hipparionines. **A.** Gansu (= Kansu) Province; Qingyang (= King-Yang) County; Locality 115. **B.** Shanxi (= Shansi) Province; Baode (= Pao-Te) County and Hequ (= Hochü) County; Localities 30, 31, 43, 44, 49, 52, 109, 110, and 114. **C.** Shanxi Province (= Shansi); Yushe–Wuxiang (= Yü-she–Wu-Hsiang) County; Localities 70 and 73. **D.** Henan (= Honan) Province; Xin-an (= Hsin-An) County; Localities 12 and 39; **E.** Shaanxi (= Shensi) Province; Fugu (= Fu-ku) County; Locality 51.

Proboscidipparion, "*Sivalhippus,*" *Pseudhipparion, Stylohipparion,* and *Cremohipparion.* Recent characterizations of these taxa can be found in MacFadden (1984), Bernor and Hussain (1985), Webb and Hulbert (1986), Hulbert (1987), Qui et al. (1987), Bernor et al. (in press) and Woodburne (1989).

***Hipparion* s.s.**—We follow MacFadden (1980, 1984), Woodburne and Bernor (1980), Woodburne et al. (1981), McFadden and Woodburne (1982), Bernor and Hussain (1985), Bernor (1985), Bernor et al. (1987), Bernor et al. (in press), and Woodburne (1989) in restricting this nomen to a specific lineage of horses that have a fossa positioned high on the face. The posterior pocket becomes reduced and eventually lost, and confluent with the adjacent facial surface (includes Group 3 of Woodburne and Bernor, 1980). We differ with some of the previous authors in the specific referrals of *Hipparion* s.s.; this issue has most recently been discussed in detail by Bernor et al. (in press).

"***Hipparion***"—Following Woodburne and Bernor (1980), MacFadden and Woodburne (1982), Bernor and Hussain (1985), Bernor (1985), Bernor et al. (1988), and Bernor et al. (in press): Old World hipparion horses with facial morphologies that differ from *Hipparion* s.s. (includes superspecific taxa listed

TABLE 1
Locality Distribution of the Uppsala Chinese Hipparionine Species

Locality number[a]	Geographic location[b]	Sampling method[c]	Taxa present (this report)[d]
12	D	2	"*H.*" *plocodus*
30	B	1	"*H.*" *forstenae*, "*H.*" *dermatorhinum*, "*H.*" ?*dermatorhinum*, hipparionine gen. and sp. indet.
31	B	1	hipparionine gen. and sp. indet.
39	D	2	*Proboscidipparion sinense*
43	B	1	"*H.*" *coelophyes*, "*H.*" aff. *coelophyes*, "*H.*" *hippidiodus*, "*H. plocodus*," hipparionine gen. and sp. indet.
44	B	1	"*H.*" *coelophyes*, "*H.*" *hippidiodus*
49	B	1	"*H. plocodus*"
51	E	2	"*H.*" ?*dermatorhinum*
52	B	1	"*H. kreugeri*," "*H.*" *hippidiodus*
70	C	2	"*H.*" *platyodus*
73	C	2	"*H.*" *ptychodus*, "*H. tylodus*"
109	B	1	"*H.*" aff. *coelophyes*
110	B	1	"*H.*" ?*dermatorhinum*
114	B	1	"*H.*" *ptychodus*
115	A	2	"*H.*" *hippidiodus*
	A	2	"*H. parvum*"

[a] Localities as used by Sefve and referred to here.
[b] Geographic province where the locality is found (see fig. 1 and its explanation for further detail).
[c] Mode of collection: 1 = tunneling; 2 = purchased from local collectors.
[d] Taxa in the Uppsala collection reported by us.

above) and belong to distinct, separate lineages.

All measurements follow AMNH recommendations as presented by Eisenmann et al., 1988, rounded to tenths of mm.

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INVESTIGATIVE HISTORY OF CHINESE HIPPARIONINES

Hipparionine remains are the most common mammalian fossils in North China, and have been used for centuries as the so-called dragon-bones or dragon-teeth of traditional

Chinese medicine. However, their first recognition as fossil horses was made at a session of the Geological Society of London (1853), when T. Davidson reported on a small suite of specimens assembled from Shanghai drugstores by W. Lockhart. According to a preliminary determination by Waterhouse, there were two hipparionine species. One was referred to the European and West Asian species common in Turolian aged faunas, *Hipparion gracile.* The other was not named, but reported as being of larger size (Koken, 1885: 4, 39). Lockhart's material was later implicitly referred by Gaudry (1873), to *Hipparion antelopinum,* and by Lydekker (1882–1883), to *Hipparion theobaldi.*

Von Richthofen made another collection from Chinese drugstores during the 1870s and assembled a large number of hipparionine teeth. Koken (1885) described 14 of these as belonging to a new species, *Hipparion richthofeni.* As has been discussed by Qui et al. (1987), and in this paper, Koken's species has subsequently caused much confusion. Here, we regard this species as a nomen dubium.

Schlosser (1903) produced the first monographic study on Chinese hipparionines. His work included a detailed description of about 850 isolated teeth and some fragmentary jaws and bones collected from Chinese drugstores by K. A. Haberer from 1899 to 1901. Schlosser referred most of these specimens to Koken's original taxon, *Hipparion richthofeni.* He also reported a limited suite of cheek teeth that belonged to a smaller morph, which he suggested was a separate species.

In 1927 Matsumoto gave a detailed description of 49 isolated teeth of unknown provenance in China. He separated these specimens into five subtaxa of *Hipparion richthofeni*: *H. richthofeni richthofeni, H. richthofeni* mut. *pater, H. richthofeni* subsp. *gigas, H. richthofeni* subsp. *dominans,* and *H. richthofeni* subsp. *pan.* Matsumoto's study drew little attention from later authors because of his extreme typological approach. The characters he considered diagnostic for his new morphs are now widely accepted as being subject to individual or ontogenetic variability. His taxon *H. richthofeni pater* appears to be the only exception. Qiu et al. (1987) argued that this taxon is virtually identical with some Yushe specimens now housed in the Tianjin Natural History Museum. They further believed that this taxon is related to the Pleistocene species *Proboscidipparion sinense,* and refer to it as *Hipparion* (*Proboscidipparion*) *pater.*

The field exploration for in situ hipparionine material began in North China in the summer of 1916, when the Swedish geologist/explorer, J. Gunnar Andersson, visited Henan and recognized the potential for discovering abundant fossil vertebrates in the Huanghe (Yellow River) Valley. Andersson secured 45,000 Swedish crowns from a wealthy patron, Lagrelius, and the following year made another large collection from Henan. In 1918 Andersson made a brief collecting trip, this time to the Mongolian border. These early years of collecting provided Andersson with enough experience and success to establish a privately funded "Kinafond" (China Fund) to pursue eight more years of fossil collecting.

In 1919, Andersson initiated a number of separate fossil collecting campaigns, including an excavation at the late Miocene locality of Ertemte, Inner Mongolia (= Nei Mongol Autonomous Region). While particularly rich in small mammals, the Ertemte Fauna also yielded a new subspecies of horse, "*Hipparion richthofeni*" race *mongolicum* (Schlosser, 1924). This subspecies was probably a composite since the specimens were collected from three sites: Ertemte, Olan Chorea, and Harr Obo. Late in the same year, Andersson sent Chang, a Chinese assistant, to Baodezhao (= Baode) to quarry fossil vertebrates. He returned some months later with 27 crates of fossils.

Andersson continued to direct expeditions to the Baode area during field seasons in 1920 and 1921, and in 1922 employed a young Austrian paleontologist, O. Zdansky, through the Palaeontologiska Institut (Uppsala, Sweden), to direct fossil collecting activities. In his first field season, Zdansky returned from Baode with no less than 100 crates of vertebrate fossils. This and previous collections from Baode constitute the majority of Uppsala hipparionine fossils described here. A detailed and highly informative account of the history of Swedish paleontological explorations in China has been given by Mateer and Lucas (1985).

While Andersson was pursuing his paleontological activities, a French Jesuit priest, E. Licent, carried out his own fossil collections. Licent worked in the Qingyang area, eastern Gansu, and reported his early discoveries in the French newspaper *La Politique de Peking* (August 1920). In October 1921, Licent selected some well-preserved and representative specimens, and sent them to the Museum National d'Histoire Naturelle, Paris. Based on this material, Teilhard de Chardin submitted a report to the Geological Society of France under the title: "Sur une faune de mammifères Pontiens provenant de la Chine septentrionale." Teilhard de Chardin simply referred these hipparionine specimens to *Hipparion richthofeni.* A recent study by Qiu et al. (1987) reported that the Qingyang locality contains only two species: *H. hippidiodus* and *H. fossatum* (= "*H.*" *coelophyes* here). One of the skulls described by Teilhard de Chardin has a nasal notch that is placed between P2 and P3, and has a tooth row 145 mm in length. Qiu et al. (1987) have judged that at least this skull may belong to *H. hippidiodus.*

In 1931 Teilhard de Chardin and C. C. Young described a new species, *Hipparion houfenense* from Jingle (Shanxi Province). This taxon is morphologically quite distinct from all those described by Sefve, and more importantly, it was collected from markedly younger horizons than the Baode localities.

Other important fossil discoveries were made in the early 1930s from the richly fossiliferous and well-stratified horizons of the Yushe Basin. In 1929 this area was explored by a technician, then of the Geological Survey of China, Liu Shi-ku. The following spring, Teilhard de Chardin and C. C. Young went to southeastern Shanxi to survey Liu's work. In 1933 and 1935 they published their initial geological and paleontological discoveries in this area. Licent followed, with the help of M. Traessert, and carried out an extensive collecting and fossil purchasing campaign throughout the Yushe Basin. Within four years, Licent and Traessert succeeded in obtaining more than 2000 well-preserved specimens. This material became the basis for a number of monographs written by Teilhard de Chardin. However, the fossil perissodactyl materials remained unstudied until recently when Qiu et al. (1987) undertook their description.

From 1930 to 1939 Childs Frick organized a collecting program in Chinese Neogene deposits through E. T. Nystrom, a Swedish Professor of Geology at the Shanxi University in Taiyuan. Two Chinese field collectors Liu Shi-ku (formerly with the Geological Survey of China), and Kan Chuan-pao ("Buckshot" of the AMNH Central Asiatic Expeditions) undertook field collections and fossil purchases from Baode, Yushe Basin and adjacent areas in Shanxi Province. The horses collected by this expedition are housed in the American Museum, and are currently being studied by Bernor and Qiu.

World War II ended scientific fossil collecting in China. Collecting activities at Yushe did not resume until 1955–56. In 1957, M. Z. Zhou reported two hipparionine teeth from near the Manas River, Xianjian Uygur Autonomous Region (Chow, 1957). Then, in 1959, Liu Houyi and Zhou Ben-xiong wrote a short note on a sample of hipparionine teeth from Lushi, Province of Henan. Also in 1959 and 1960, a Sino-Soviet Paleontological Expedition was organized to the Nei Mongol Autonomous Region. During this expedition, several samples of hipparionine fossils were gathered from a total of five localities: Tuchengzi and Heishatu of Huade County; Heidaigou and Yaogou of the Jungar Banner; and Wudu, Province of Gansu.

During the 1960s a number of hipparion discoveries were made. The most significant were those from the Lantian area. A systematic excavation was conducted during field collections made between 1963 and 1965. The material comprises more than 50 skulls and jaws, and a large number of isolated teeth and limb bones. The material was studied before the Cultural Revolution, but not published until much later (Liu et al., 1978).

Several important discoveries of hipparionine fossils were made in the 1970s. In 1972, a field party from the IVPP discovered two hipparionine skulls and some jaws at the locality of Anle, Huoxian County, Shanxi. Qiu et al. (1987) reported their referral to *Hipparion forstenae* and *Hipparion* cf. *houfenense.* In 1975, the first hipparionines from the Tibetan plateau were discovered. They included two new species: *Hipparion qui-*

zhongensis Ji Hong-xian et al., 1980, from Buron Basin and *Hipparion xizangense* Zheng Shao-hua, 1980 from Biru County. In 1975 hipparionine fossils were also found at Lufeng, Yunnan, a site famous for its abundant late Miocene hominoid fossils. Qi Guo-quin (1977) briefly described the Lufeng hipparionines, referring them to the Siwalik taxon *Hipparion nagriense.*

A number of investigators have subsequently referred to the Chinese material in passing, but none so far has attempted to grapple directly with the alpha-level systematics of the Uppsala assemblage. Gromova (1952) claimed that she could consider only three of Sefve's (1927) species as being valid. Forsten (1968) originally recognized no more than five. In a recent paper, Forsten (1985) briefly reviewed the Uppsala collection and again recognized five of Sefve's (1927) original species: "*H.*" *dermatorhinum,* "*H.*" *hippidiodus,* "*H.*" *plocodus,* "*H.*" *coelophyes,* and *Proboscidipparion sinense.* In addition she erected a new species, *Hipparion sefvei,* based on a metacarpal III. We believe the recognition of this last taxon was inappropriate because of the inadequacy of the type material.

Although Forsten's (1985) latest work did give a review of fossil material by locality, and designated lectotypes, her work did not describe individual specimens, it did not make clear species referrals of specimens other than her lectotypes, and it did not give the measurements of characters she used to unite specimens in given taxa. Furthermore, while Forsten (1985) referred lower jaw and postcranial materials to Sefve's (1927) species, she failed to give either morphological or statistical reasons for doing so, apparently depending on their common locality provenance alone. This practice is particularly periolous since several taxa, often overlapping in their size, are known to occur at many localities.

Table 1 gives the locality distribution of the Palaeontologiska Museet Chinese hipparions. Also recorded in this table are the modes of fossil collection. For the hipparionine specimens under consideration here, there were two modes of sampling: (1) tunneling supervised by Zdansky (as described by Zdansky, 1923), and (2) by purchasing from local collectors. This sample includes no specimens that were quarried from surface exposures. Zdansky (1923) has elaborated on the tunneling activities which he supervised at Baode. He had local laborers produce accurate maps of the gallery networks, recording and eventually publishing the various localities' provenance (Zdansky, 1923). These records are sufficiently accurate to consider these samples as being single quarry samples (Tedford, personal commun.). This is particularly important when considering the validity of our morphological groups as being or not being single paleo-"population" samples (see discussion under Methods).

METHODS

Gromova (1952) has often been cited as setting the methodological standards for studying hipparionines, having emphasized the use of both qualitative and quantitative skeletal characters. Most subsequent workers have relied either on morphological analyses and evolutionary systematics or statistical analyses and phenetic systematics. A historical review of these different approaches has recently been given by Bernor and Hussain (1985).

Bernor and Hussain (1985), Bernor (1985), and Bernor et al. (in press) have endeavored to bridge the obvious methodological hiatus between these two schools of thought by combining studies of cranial and postcranial morphology with an extensive suite of measurements in a series of systematic, evolutionary, and biogeographic analyses of Old World hipparionines. Theirs and other recent analyses of hipparionine cranial and dental morphology have demonstrated that taxonomic groups of specific and superspecific rank can be recognized by using discrete character states. Species so recognized have been subsequently used for a variety of geological and paleobiological studies.

The purpose of this contribution is to formally designate the PMU lectotypes, refer their PMU hypodigms, and describe those recently prepared AMNH specimens which are referable to the type series. The two collections include a large series of virtually complete skulls, skull fragments, mandibles, isolated maxillary and mandibular teeth, and

TABLE 2

Hipparionine Character States (after Bernor et al., in press)

(1) Relationship of lacrimal to preorbital fossa: a = lacrimal large, rectangularly shaped, invades medial wall and posterior aspect of preorbital fossa; b = lacrimal reduced in size, slightly invades or touches posterior border of preorbital fossa; c = preorbital bar (POB) long with anterior edge of lacrimal placed more than half the distance from anterior orbital rim to posterior rim of fossa; d = POB reduced slightly in length but with anterior edge of lacrimal placed more than half the distance from anterior orbital rim to posterior rim of fossa; e = POB vestigial, but lacrimal as in d; f = POB absent; g = POB very long with anterior edge of lacrimal placed less than half the distance from anterior orbital rim to posterior rim of fossa; h = POB absent

(2) Orbital surface of lacrimal bone: a = with foramen; b = lacking foramen.

(3) Preorbital fossa morphology: a = large, ovoid shape, anteroposteriorly oriented; b = subtriangular shaped and anteroventrally oriented; c = subtriangular shaped and anteroposteriorly oriented; d = egg-shaped and anteroposteriorly oriented; e = C-shaped and anteroposteriorly oriented; f = vestigial but with a C-shaped or egg-shaped outline; g = vestigial without C-shape outline, or absent; h = elongate, anteroposteriorly oriented; i = morphology as in h, but with faint peripheral rim; j = small, rounded structure; k = posterior rim straight, with nonoriented medial depression.

(4) Fossa posterior pocketing: a = deeply pocketed, greater than 15 mm in deepest place; b = pocketing reduced, moderate to slight depth, less than 15 mm; c = not pocketed but with a posterior rim; d = absent, no rim but a remnant depression; e = absent.

(5) Fossa medial depth: a = deep, greater than 15 mm in deepest place; b = moderate depth, 10–15 mm in deepest place; c = shallow depth, less than 10 mm in deepest place; d = absent.

(6) Preorbital fossa medial wall morphology: a = without internal pits; b = with internal pits.

(7) Fossa peripheral border outline; a = strong, strongly delineated around entire periphery; b = moderately delineated around periphery; c = weakly defined around periphery; d = absent with a remnant depression; e = absent, no remnant depression.

(8) Anterior rim morphology: a = present; b = absent.

(9) Placement of infraorbital foramen: a = placed distinctly ventral to approximately half the distance between the preorbital fossa's anteriormost and posteriormost extent; b = inferior to or encroaching on anteroventral border or the preorbital fossa.

(10) Confluence of buccinator and canine fossae: a = present; b = absent, buccinator fossa is distinctly delimited.

(11) Buccinator fossa: a = unpocketed posteriorly; b = pocketed posteriorly.

(12) Caninus (= intermediate) fossa: a = absent; b = present.

(13) Malar fossa: a = absent; b = present.

(14) Nasal notch position: a = at posterior border of canine or slightly posterior to canine border; b = approximately half the distance between canine and P2; c = at or near the anterior border of P2; d = above P2; e = above P3; f = above P4; g = above M1; h = posterior to M1.

(15) Presence of P1: a = present, persistent and functional; b = impersistent or absent.

(16) Curvature of maxillary cheek teeth: a = very curved; b = moderately curved or straight.

(17) Cheek tooth crown height: a = <30 mm maximum crown height; b = 30–40 mm maximum crown height; c = 40–60 mm maximum crown height; d = >60 mm maximum crown height.

(18) Maxillary cheek tooth fossette ornamentation: a = complex, with several deeply amplified plications; b = moderately complex with fewer, more shortly amplified, thinly banded plications; c = simple complexity with few, shortly amplified plications; d = generally no plis.

(19) Posterior wall of postfossette: a = may not be distinct; b = always distinct.

(20) Pli caballin morphology: a = double; b = single; c = complex; d = plis not well formed.

(21) Hypoglyph: a = hypocone encircled by hypoglyph; b = deeply incised, may occasionally close, isolating hypocone; c = moderately deeply incised; d = shallowly incised.

(22) Protocone shape: a = elongate-oval; b = lingually flattened–labially rounded; c = oval; d = rounded; e = triangular; f = triangular-elongate; g = lenticular.

(23) Isolation of protocone: a = connected to protoloph; b = isolated from protoloph.

(24) Protoconal spur: a = elongate, strongly present; b = reduced, but usually present; c = very rare to absent.

(25) Protocone/hypocone alignment: a = anteroposteriorly aligned; b = protocone more lingually placed.

(26) P2 anterostyle/paraconid: a = elongate; b = short and rounded.

(27) Mandibular incisor morphology: a = not grooved; b = grooved.

(28) Mandibular incisor curvature: a = curved; b = straight.

(29) I3 lateral aspect: a = elongate, not transversely constricted; b = very elongate, transversely constricted (atrophied).

(30) Premolar metaconid: a = rounded; b = elongated; c = angular on distal surface.

TABLE 2—(*Continued*)

(31) Molar metaconid: a = rounded; b = elongated; c = angular on distal surface.
(32) Premolar metastylid: a = rounded; b = elongate; c = angular on proximal surface.
(33) Molar metastylid: a = rounded; b = elongate; c = angular on proximal surface.
(34) Premolar ectoflexid: a = does not separate metaconid and metastylid; b = separates metaconid and metastylid.
(35) Molar ectoflexid: a = does not separate metaconid and metastylid; b = separates metaconid and metastylid.
(36) Pli caballinid: a = complex; b = rudimentary or single; c = absent.
(37) Protostylid: a = present, but not columnar; b = rare to absent; c = strong, columnar.
(38) Ectostylids: a = present; b = absent.
(39) Premolar linguaflexid: a = shallow; b = V-shaped; c = shallow U-shaped; d = deep, broad U-shape.
(40) Molar linguaflexid: a = shallow; b = V-shaped; c = shallow U-shaped; d = deep U-shaped

postcranial elements. There are no articulated skeletons, and most localities include two or more hipparionine species. We have elected to recognize formal species in the PMU collection based on skull and directly associated mandibular morphology only because they contain the most morphological information relevant to systematic and phylogenetic considerations, they constitute the sole elements used by Sefve in his species designations, and because there can be no certain referral of isolated cranial and postcranial fragments to any given taxon. The *inferential* referral of isolated dentitions and postcranial remains can be made in the future, building upon the baseline morphological and statistical analyses provided in this and methologically similar studies.

The principal systematic methodology employed here is an analysis of discrete morphological character state distribution. Through a series of hipparionine studies (Woodburne and Bernor, 1980; Bernor et al., 1980; MacFadden, 1984; Webb and Hulbert, 1986; Hulbert, 1987; Bernor and Hussain, 1985; Bernor, 1985; Bernor et al., 1988; Bernor et al., in press), a number of skeletal character complexes have been recognized as a series of two or more states per character. These multistate characters have been found to be reasonably homogeneous within adult individuals of a single species. Species shown to be united by a constellation of uniquely shared-derived characters have been taken as being phylogenetically related.

Our character state analysis first proceeds on the skull and directly associated mandibular sample (the latter being uncommon), by recording discrete states for each of the 40 morphological variables under consideration (table 2). Morphological groups are then assembled based on their shared character states. Age of individual is recorded and used for discriminating ontogenetically dependent variability. Since cheek teeth particularly transform their patterns of enamel ornamentation during ontogeny (Bernor and Hussain, 1985; Bernor, 1985), we use, wherever feasible, the adult middle stage of wear for species characterization. We avoid making a formal phylogenetic analysis because of our desire to complete the preparation, analysis, and description of the large AMNH and IVPP collections before finalizing our evolutionary interpretations. However, we do provide judiciously considered phylogenetic interpretations of these species based on currently available data.

A number of the 40 characters we use are either believed by Bernor to be shared-derived among all Old World hipparions (i.e., characters 2b, 9b, 10b, 15b, 16b, 17c–d, 19b, 23b, 24c, 25b) or not occurring in the taxa we describe here (6a, 11b, 13b, 26a, 28a, 29a, and 38b). While we record these states in table 3, we do not repeat them in our diagnoses or descriptions. Additionally, we record the character state distribution for each skull we describe in Appendix 1, and each mandible in Appendix 2. The reader is referred to Bernor et al. (in press) for illustration and evaluation of these characters, and a summary of the broader evolutionary history of Old World lineages.

Because of the two different modes of specimen sampling (by tunneling and by purchase from local collectors; table 1), we are not treating the morphological groups as being geologically and chronologically "homogeneous" quarry samples; not all of them are.

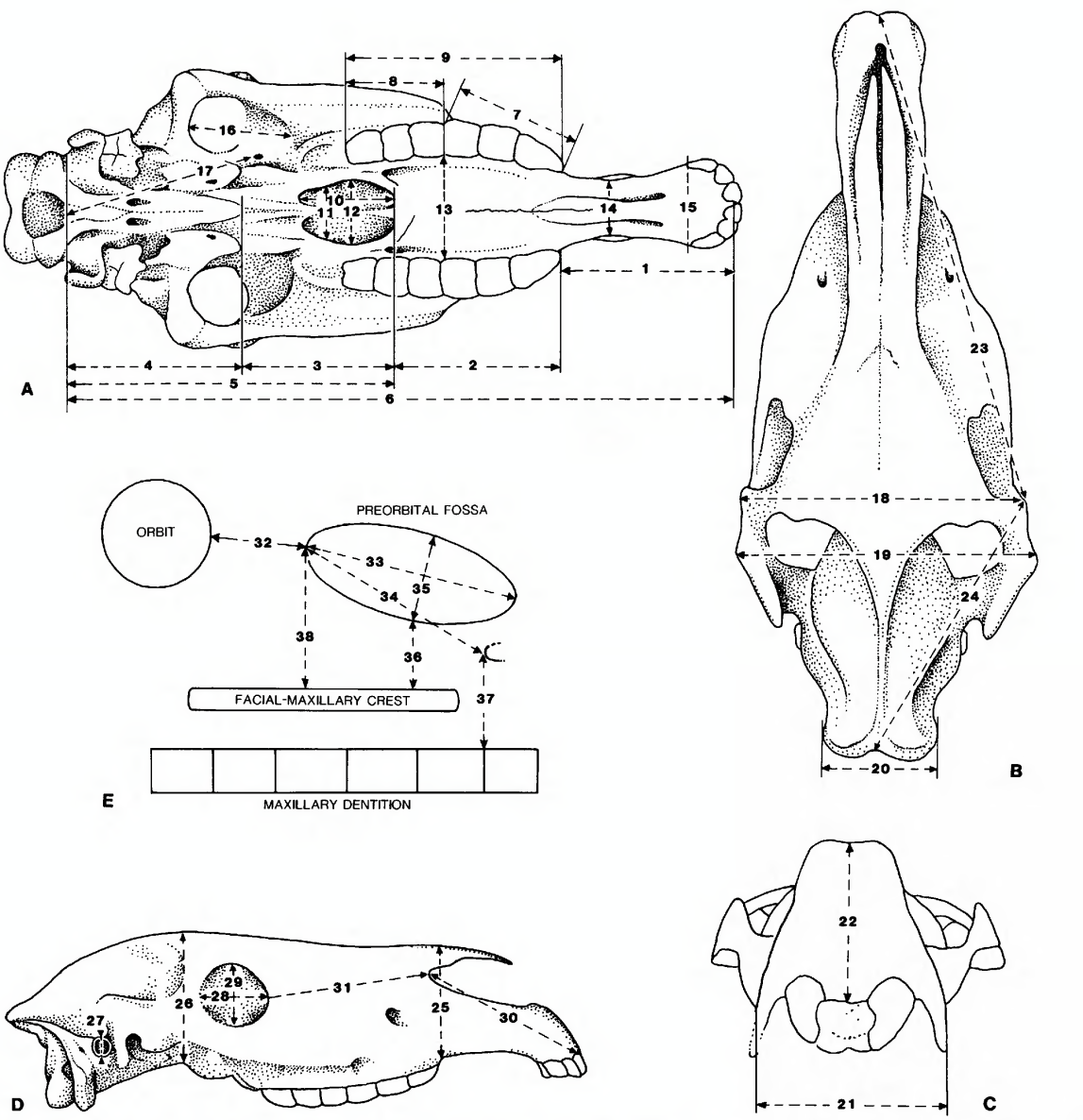

Fig. 2. Conventions for measured cranial characters. **A.** Ventral view of skull. **B.** Dorsal view of skull. **C.** Occipital view of skull. **D.** Lateral view of skull. **E.** Schematic of facial fossa position with respect to facial-maxillary crest and maxillary dentition.

Rather, we treat our morphological groups as populations bound by discretely shared characters, and attempt to test this hypothesis statistically.

Eisenmann et al. (1988) have outlined methods for measuring fossil hipparionine skulls (fig. 2) and mandibles (fig. 3), after recommendations of the American Museum Symposium on Equid Systematics. We present all measurements on skulls in table 4 and associated mandible measurements in table 5. Because of the great page length of our parametric statistical test results, these data have been placed on IBM 5¼ in. computer disc, filed in the AMNH Osborn Library, and will be made available to any interested worker. Disc table 1 gives parametric summary statistics for each skull variable by species. Disc table 2 gives a summary of the statistical skull comparisons of the Uppsala

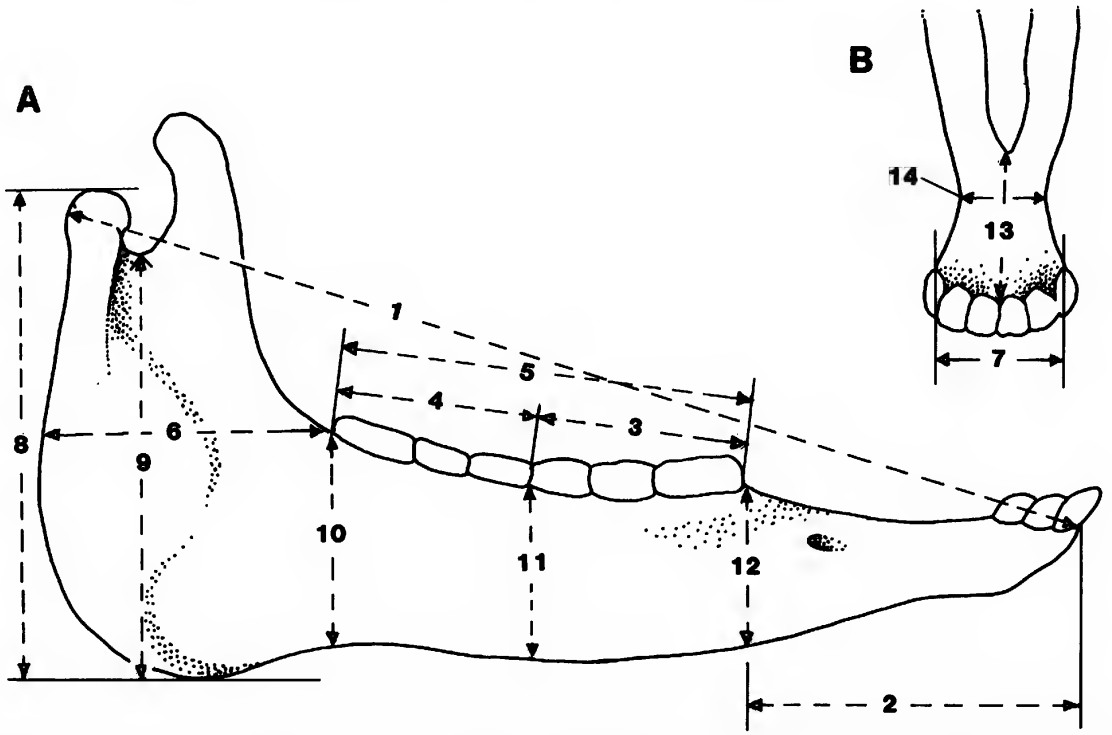

Fig. 3. Conventions for measured mandibular characters. **A.** Lateral view of mandible. **B.** Ventral view of mandibular symphysis.

Chinese hipparionines to the Höwenegg quarry sample population. Disc table 3 includes individual maxillary cheek tooth measurements and character state scores of the Uppsala specimens. Disc table 4 summarizes the statistical comparisons, by individual skull variable, between all Chinese morphs and the Höwenegg quarry population.

CHARACTER STATE AND STATISTICAL ANALYSES

CHARACTER STATE ANALYSIS: Appendices 1 and 2 summarize character states for all skull, maxillary, and mandibular material referred to in this text. Computer Disc table 3 gives measurement and character state distribution for each tooth in the upper dentition. These characters follow the definition in Bernor et al. (in press), and are recorded as unordered states (a, b, c, . . . etc.). When a character state is followed by a slash (/), we record a state that is either intermediate (i.e., a/ is intermediate between states a and b), or variably expressed (a and b) in the species hypodigm. These tables have ordered specimens into morphological groups based on their shared states. Morphological groups have been crosschecked by size comparisons and the stage of cheek tooth wear was evaluated so that a given specimen was not excluded from a group because of ontogenetic variation.

The morphological groups which we have recognized include: (1) PMU M3691 with cf. referral of AMNH 91 B979; (2) PMU M3685; (3) PMU M3688, M3690, M311, M309, M3689, M584, M594, M590 (note specific referrals here in the text); (4) PMU M3819, M249, M596, M595, M247, M248, M250, M3818, M251, M252 and M253; (5) PMU M347, M3684, M593, M350; (6) PMU M3872, M260, M258/259, M261, AMNH 41 L310; (7) PMU M3873, M269, M3820, M267, M268, M585, M592, M591, M586, M7357, M7362, M7359, AMNH 41 L352, AMNH 18 278, AMNH 19 L81, AMNH 41 L333; (8) PMU M3925; (9) PMU M3824, M3825, M348; (10) PMU M3864; (11) PMU M3821 A + B. The remainder of the specimens listed in Appendices 1 and 2 could not be referred to any specific morphological

TABLE 3
Summary Character State Distributions of Uppsala Chinese Hipparionine Skulls

Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
"*H.*" *platyodus* EA, 9.5–5 Ma	C	B	B	B/	B	A	B	A	B	B	A	A	A	C	B	B
"*H.*" *coelophyes* EA, 8 Ma	C	B	D	C	B/	A	B/	B	B	B	A	A	A	C	B	B
"*H.*" *hippidiodus* EA, 8–6 Ma	E	B	G	D	C	A	D	B	B	B	A	A	A		B	B
"*H.*" *ptychodus* EA, 8–4.5 Ma	G	B	J	B	A	A	B	A	B	B	A	A	A	?C	B	B
"*H.*" *dermatorhinum* EA, 10–7.5 Ma	D	B	B	B	B	A	A	A	B	B	A	A	A	F	B	B
"*H.*" *forstenae* EA, 9–7.5 Ma	B	B	B	C	C	A	C	B	B	B	A	B	A	D/	B	B
P. sinense EA, 3–2 Ma	H	B	G	E	D	A	E	B	B	B	A	A	A	H	B	B
"*H. plocodus*"																
"*H. tylodus*"																
"*H. parvum*"																

Legend: Taxa: as in text, NA = North America, Eu = Europe, SWA = Southwest Asia (includes Greek and Western U.S.S.R. localities), NAf = North Africa, EA = East Asia, SA = South Asia.

group. A detailed accounting of the characters that unite these groups, the justification for these groups' distinction as species, the range of morphological variability within species hypodigms and apparent species relationships are discussed under Systematics.

STATISTICAL ANALYSIS: Descriptive parametric statistics on 38 skull characters were calculated for the 11 groups of fossil specimens segregated as morphologically distinct, or potentially distinct, in the preceding character state analysis. These statistical measures included: mean, standard deviation, lower and upper 95 percent mean confidence limits, coefficient of variation, standard error of the coefficient of variation, minimum, maximum, and median measurements. 95 percent confidence intervals were calculated for any sample size larger than two, and upper and lower limits are reported in Disc table 1; summaries of these results have been tabulated in Disc table 2. Our attempts to calculate multivariate statistics have been thwarted by small sample sizes and missing values.

We have used the 11 million-year-old quarry sample of "*Hipparion*" *primigenium* from Höwenegg, Germany (Bernor et al., in prep.), as a baseline standard for paleospecies comparison. The Höwenegg sample is an extraordinary one, including 14 complete to partial skeletons (Tobien, 1986). However, our skull data include some variables we acknowledge as being problematic due to mediolateral crushing. We are not aware of any other hipparionine sample which fulfills the desirable criteria of having complete articulated skeletons of a single species gathered from a chronologically restricted single quarry sample. A complete description and statistical evalulation of the Höwenegg hipparionine sample is currently in progress.

SYSTEMATICS

ORDER PERISSODACTYLA OWEN 1848
SUBORDER HIPPOMORPHA WOOD 1937
SUPERFAMILY EQUOIDEA HAY 1902
FAMILY EQUIDAE GRAY 1821
SUBFAMILY EQUINAE STEINMANN AND DODERLEIN 1890

"*Hipparion*" *platyodus* Sefve, 1927

Hipparion platyodus Sefve, 1927: 34, pl. VI, fig. 21.

LECTOTYPE: PMU M3691.

LECTOTYPE LOCALITY: Locality 70, Wuxiang County, Shanxi (Zdansky, 1923).

AGE: Late Miocene–early Pliocene.

GEOGRAPHIC RANGE: Qinggou, Xigoucun, Wuxiang County, Shanxi, China.

DIAGNOSIS: Medium-size hipparionine species; snout short; POB long (43.6 mm), lacrimal placed posterior to POF; POF subtriangular shaped, anteroposteriorly oriented, slightly pocketed posteriorly, medial depth moderate, anterior rim faint but distinct, peripheral border outline moderately strongly expressed; nasal notch retracted to P2; maxillary cheek tooth row 149.2 mm in length,

TABLE 3—(*Extended*)

	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
	C	A	B	A	B	B	B	C	B	A	A	A	A	C	C	C	C	A	B	B/	A	B	A	D
	C	A	B	A	B	B	B	C	B	A														
	C	B/	B	B	C/	C/	B	C	B	A														
	C	A+/B		A/	B	B	B	C	B	A														
	C	A	B	A/	B	G	B	C	B	A	A	A	A	B	B	B	B	A	B	B	A/	B/	A/	C
	C	B	B	A/	C/	C/	B	C	B	A														
	D	A+	B	C	B	F	B	C	B	A	A	A	A	C	C	C	C	A	B	C	B	B	D	D
"*H. plocodus*"																								
"*H. tylodus*"																								
"*H. parvum*"																								

with complexly plicated fossettes, pli caballins double or complex, hypoglyphs deeply incised, protocones with distinct lingual flattening and labial rounding; mandibular cheek teeth with occasional and weakly developed pli caballinids, protostylids strongly developed on all cheek teeth except p2, linguaflexids shallow on premolars, deep and broadly U-shaped on molars; metaconids, and metastylids usually with angular opposing borders; entoflexids and metaflexids often with complex enamel borders.

DESCRIPTION: The lectotype, PMU M3691, a virtually complete adult male skull lacking a small portion of the posterior cranium, a piece of the right nasal, left posterior and inferior orbital rim and left zygomatic bone (fig. 4). It is a moderate-size horse with a relatively short snout. The preorbital bar is long and the lacrimal is placed distinctly posterior to the preorbital fossa's posterior rim, although less than half the distance from the posterior border of the fossa to the orbit. The fossa is moderately long, subtriangularly shaped, and anteroventrally oriented. It has slight posterior pocketing, moderate medial depth, anterior rim is faint, its peripheral outline is moderately well expressed and its ventral border has a regular contour. Dorsoventral height of POF is significantly greater than the distance from the facial-maxillary crest to its ventral border. The buccinator fossa is medially deep. The infraorbital foramen is just above the horizontal plane described by the facial-maxillary crest, at the anteroventral border of the preorbital fossa. Nasal notch is retracted to the anterior limit of P2. The incisors have large, elongate infundibula. The canines are stout, with a smooth convex labial border and a lingual surface which has a stout central pillar flanked anteriorly and posteriorly by small distinct recesses. The cheek teeth all have complex plications of the pre- and postfossettes, pli caballins are usually bifid or complex, hypoglyphs are deeply incised and all protocones are lingually flattened and labially rounded.

PMU M3691 has an associated mandible which is virtually complete including incisors, canines, and all the cheek teeth except the left m3. The mandibular corpus is complete back to the molar teeth, then is broken and lacking the ventral border along with the ascending rami. The incisors and canine teeth are essentially as in their maxillary homologs. The premolar cheek teeth all have short ectoflexids which do not separate the metaconids/metastylids. Metaconids are rounded on p2 only, having angular posterior borders on p3–4, metastylids have marked angular posterior borders on all premolars. There is a rudimentary pli caballinid on p2, a single one on p3 and none on p4; protostylids are present and large on p3–4, lacking on p2. Linguaflexids are shallow on all premolars. Entoflexids are elongate and have complex anteriormost borders where they separate metaconid/metastylid on p2–3 only; p2 metaflexid is elongate and transversely narrow, whereas on p3–4 they are square and have complex enamel borders. The molar teeth have ectoflexids separating metaconids/metaflexids on m1–2 but not m3. Molars have angular facing borders of metaconids/metastylids. There are no pli caballinids. Linguaflexids are deeply incised and broadly

TABLE 4
Measurements on Uppsala Chinese Hipparionine Skulls

Measurement	M3691	M3685	M3688	M311	M3690	M309	M3689	M584
1	98.8		88.9			91.5		103.3
2	111.7		99.6	98.1	104.5	99.5	97.0	105.7
3	84.6		e90	95.4			84.8	90.9
4				77.0				
5				169.2				
6								
7	82.5	60.1	68.3	71.6	74.5	75.7	56.0	79.5
8	66.5	60.7	59.5	57.8	60.4	61.5		63.3
9	149.2	131.3	125.7	128.5	134.9	134.4		140.7
10	51.6		45.0	45.7	66.1	46.9	37.6	57.2
11	29.7			29.5	26.1	25.4	29.1	33.0
12	31.8			36.5	29.0	34.3	32.7	38.5
13	56.8	66.2	60.8	63.3	e49	57.8	62.2	61.7
14	33.5	41.9	29.5		25.5	28.1		34.1
15	45.7		37.8		30.7	26.3		47.6
16	77.5		56.7	62.9				62.0
17				92.5				
18	e142		106.5					140.6
19	e171		147.4					163.9
20								
21								
22				e85				
23	292.4		260.7	e249	e284	e291		
24								
25	78.1	e89	50.5	e61	81.2			e82
26	80.7		88.1	68.0			67.3	90.3
27								
28	55.5		45.0					56.7
29	48.8		47.5		50.3	45.6	47.8	48.5
30	113.5		87.7		e87			138.5
31	149.1		142.0		140			121.0
32	43.6	37.0	46.2	44.7	42.2	41.7		30.7
33	70.3	53.6	65.5	59.9	58.9			65.2
34	64.1	54.2			59.5			68.6
35	49.7	57.5	24.8	23.6	33.2	31.2		42.3
36	17.5	26.0	19.5	25.0	27.6	32.7		20.9
37	24.6	40.0			44.2			45.8
38	43.6	46.0	38.8	39.0	41.7	39.2		40.3

	M594	M590	M3819	M249	M596	M595	M347	M3684
1								102.5
2		93.6	114.2				91.2	106.8
3						72.9	121.0	
4								
5								
6								
7		77.2	81.1	84.7			73.0	76.3
8	60.0		68.3		67.0		62.2	62.8
9			147.9				134.8	136.8
10			74.5		62.2	46.5	70.7	e61
11			35.0		31.8	32.1	32.8	38.8
12	e37		37.6		33.4	31.8	35.7	38.1
13	63.0	67.1	64.2	71.8	e62	60.5	68.6	66.0

TABLE 4—(*Continued*)

Measurement	M594	M590	M3819	M249	M596	M595	M347	M3684
14							e42	34.0
15								44.7
16						65.4	78.0	
17							e121	
18							e148	
19							e181	
20								
21								
22								
23								284.8
24								
25							e89	80.7
26							e105	
27								
28						60.0	56.1	
29				e49		45.5	45.8	
30								
31								
32			29.0		40.5	33.0	50.2	e47
33							55.4	47.6
34							60.3	60.7
35							33.3	27.9
36							38.8	29.5
37				36.3			54.7	37.6
38					46.5	41.8	59.1	46.4
	M593	M350	M3872	M260	M3873	M269	M3820	M267
1			114.5					
2	111.9	99.6	e115	98.2	112.1	97.0		99.8
3		97.0	e113		95.8			104.9
4			e90		82.1			68.3
5			e194		174.0			168.6
6			e427					
7	75.3	77.2	e90.0	90.4	73.9	63.8	73.6	82.5
8	67.1				62.0	53.3	58.4	66.5
9	142.2				134.7	117.8	131.2	145.6
10	65.8	56.5	e49	54.8	56.9	53.7	65.2	50.0
11	e22	29.5	e33.2	32.0	29.2	35.4	26.7	30.5
12	e31	31.2	e35.1	35.5	28.4	37.6	30.2	34.1
13	28.3	53.4	e65.0	66.5	62.1	56.4	64.0	65.5
14			36.8		33.7	32.4		
15			e36					
16			73.7		67.8			
17			e115		e88			85.7
18	e63	e117	137.4		e152	136.7		
19		e146	e179		162.4			
20								
21								
22					58.4			53.7
23			327.4		e313	e284		
24			173.2		156.3			
25	e89	e65.4	106.5		102.9			
26		e74	84.7		88.0			

TABLE 4—(*Continued*)

Measurement	M593	M350	M3872	M260	M3873	M269	M3820	M267
27								
28	58.1	54.6	66.0	56.2	58.0	e53		
29	45.3	55.1	43.2	e42	49.0	45.5	e46	
30			195.9		e158			
31			92.2		132.2			
32	44.7	41.6	37.3	32.4	33.0	27.0	e21.5	35.1
33	60.1	65.3	64.3	58.2	64.2	62.9	66.8	
34	65.2		68.9	48.4				
35	37.7	31.0	35.4	57.8	48.4	54.0	47.5	
36	40.8	24.3	23.9	29.7	23.4	11.8	24.6	
37	29.8		e53	50.2		46.6		
38	57.4	57.8	49.4	61.7	39.9		44.4	37.0
	M268	M585	M592	M591	M586	M7357	M7362	M7359
1		95.2						
2	104.3	85.8	103.3	96.5	108.5	96.4		e115
3		79.0						
4							94.8	
5								
6								
7	77.0	75.3	70.7	66.6	57.5	69.1		
8	61.2	57.4	57.0			56.9		67.2
9	e135	120.0	126.3			124.1		
10	64.6	61.6			52.8	e34.2		142.8
11	40.3	35.2	34.1		35.1	33.8		26.5
12	38.9	36.9	36.3	e39	35.7			30.9
13	66.8	e35	e60	e65	65.8			
14		32.7		38.8				
15		42.6						
16		60.7			59.5			
17								
18	e143							
19								
20								
21				e91				
22								
23		289.5						
24								
25								
26								
27								
28		53.5	51.7		55.0		52.4	
29	48.7	43.8	48.2		47.5		46.4	
30								
31				117.4				
32	24.2	26.0	32.9	e32.5	26.0	30.7		
33	68.1	e54		52.8	64.5	50.6		
34	65.8					58.4		
35	43.4	47.3		54.1	56.5	41.2		
36	22.8	23.3		28.0	20.9	27.0		e21
37	21.6					56.7		
38	41.6	41.3	43.9	54.5	e53	81.8	52.6	

TABLE 4—(*Continued*)

Measurement	M588	M3821	M3925	M3824	M348	M3864
1		105.8	127.7	118.7		
2	87.8	97.1	145.3	103.2	86.7	100.7
3	92.6	97.6	116.1			94.4
4		80.6	113.8			
5		174.8	226.5			
6		379	501.0			
7		64.8	88.9	75.8	74.5	75.6
8		56.2	76.0	59.2	61.5	60.3
9		120.5	164.5	134.0	132.6	135.6
10	56.3	e43	55.2		e50	55.4
11	26.4	23.7	36.6		e35	37.8
12	28.7	24.1	41.8		e37	39.5
13	57.4		74.4	68.9	70.5	66.0
14		24.3	39.1	32.6		30.4
15		38.4	57.7	40.3		47.4
16	66.2	60.5	80.6			
17		98.0	119.6			
18	132.0	e121	175.3			
19	147.8	145.5	199.5			
20						
21						
22		61.8	69.7			
23		292.6	390.4			
24		156.0	e179			
25			67.5			
26	72.9	92.6	76.5			
27						
28	e51	52.3	65.2			
29		48.9				
30						
31	121.4					
32	33.1	34.4				
33		48.8				
34		49.9				
35		34.8				
36		36.0			26.7	20.4
37		33.8				
38	43.8	47.7				

AMNH Skull Specimens

Measurement	91 B979	41 L310	41 L352	BX18 278	BX19 L81	41 L333
1	115.9	118.2	108.4	97.6		93.1
2	97.6	102.5	101.8	77.1	82.8	
3		106.9	94.0	81.8	82.3	
4		82.5	83.4	76.8		
5	176.7	188.2	170.1			
6	388.9	411.4	380.6			324.0
7	74.6	82.8	67.6	85.1	83.9	87.8
8	61.8	66.0	57.5			
9	134.8	150.1	125.1			

TABLE 4—(*Continued*)

Measurement	91 B979	41 L310	41 L352	BX18 278	BX19 L81	41 L333
10	59.9	64.2	58.9	63.4	60.9	
11	31.5	26.7	34.1	29.5	30.1	
12	29.0	33.0	34.3	28.7	31.2	
13	45.2	63.0	57.7	51.4	51.0	
14	24.4	35.2	34.5	26.2		
15	33.4	41.6	44.4	42.0		
16						
17						
18	105.3	123.2		107.5	125.5	113.5
19	126.5					@126
20	42.4			54.8		
21						
22	59.2					63.0
23	287.9	306.6	294.1	256.8		255.3
24	179.0			143.0		151.1
25	96.6		85.3	78.7	66.8	77.8
26	95.5	114.3		88.1	77.9	94.2
27						
28	57.1	57.0				50.2
29	50.4	49.3	44.8	43.6	42.3	40.0
30	127.7	187.5	147.3	134.5		129.5
31	127.4	99.4	123.1	98.6	110.8	102.9
32	42.5	43.6	25.8	22.3	23.9	25.5
33	50.8	66.6	66.0	55.0	57.9	51.1
34	55.3	73.8	58.6	56.0	49.2	45.0
35	31.0	26.5				41.0
36	29.2	26.7				18.6
37	53.8	49.0	52.9	40.5	42.4	40.9
38	72.4	88.5	74.3	53.7	60.6	64.1

U-shaped on m1–2, but not m3. Entoflexids are elongate and only m3 has a complex border. Metaflexids are square and have complex borders on all molars.

There is a single, well-preserved and virtually complete prepared skull and mandible of an adult male in the American Museum, 91 B979 (fig. 5), which we refer to "*H.*" cf. *platyodus*. The skull differs from PMU M3691 only in its lesser POF posterior pocketing, slightly shallower medial depth, lack of an anterior rim, and somewhat less complex plication of cheek tooth fossettes. Yet in essential features of the face, including nasal notch incisure, placement of POF with respect to orbit, lacrimal, and maxillary crest, and maxillary tooth morphology, 91 B979 compares quite closely with "*H.*" *platyodus*.

The mandible of 91 B979 differs from that of PMU M3691 in its more rounded premolar metaconid and metastylid facing borders, lack of pli caballinids on all cheek teeth, and shallower molar linguaflexids. These cheek tooth features may or may not be wear related.

DISCUSSION: No other specimens in the PMU collection, or currently prepared AMNH specimens are readily referable to "*H.*" *platyodus*. However, another specimen, PMU M3685, shows some similarities in its facial morphology. PMU M3685 is a very old adult male that Sefve (1927: pl. V, fig. 19) figured and informally named *H. kreugeri*. This specimen is not so well preserved as PMU M3691, lacking most of the orbits and snout. Also, the cheek teeth are in a very late stage of wear and have occlusal details altered considerably beyond those typical in middle adult wear.

PMU M3685 is similar to "*H.*" *platyodus*

in preorbital fossa shape, orientation, and medial depth. It differs from "*H.*" *platyodus* in its shorter preorbital bar (37 vs. 43.6 mm), lesser anteroposterior length (53.6 vs. 70.3 mm) and greater dorsoventral height (57.5 vs. 49.7 mm) of the fossa, and greater distance from the fossa's ventral border to the facial maxillary crest (26.0 vs. 17.5 mm). The infraorbital foramen is placed higher (40.0 vs. 24.6 mm) and more posterior relative to the preorbital fossa than in PMU M3691. However, it should be noted that none of these five measurement differences can be tested for statistical significance because of their small sample size (N = 1 for each morphogroup). Numerically, the cheek tooth dimensions (variables 7, 8, and 9) are shorter, perhaps largely due to their advanced stage of wear. But again, sample sizes are not large enough to test their statistical significance. Cheek tooth wear could also account for the sharply reduced plication amplitude of the pre- and postfossettes, obliteration of the pli caballins, decreased hypoglyph incision, rounding of the protocone and joining of the protocone with the protoloph (except M3) seen in "*Hipparion*" *kreugeri.*

Qiu et al. (1987) have considered the taxonomic affinities of "*Hipparion kreugeri*" in some detail and proposed that it is synonymous with "*Hipparion*" *hippidiodus* based on similarity in the maxillary cheek teeth: rounded protocone, relatively simple ornamentation of fossettes and pli caballin. The authors noted the highly reduced to absent preorbital fossa in "*Hipparion*" *hippidiodus,* but believed that the range of variability within this species may include "*Hipparion*" *kreugeri.* Qiu et al. (1987) also argued that the metapodials from Locality 52, where "*Hipparion*" *kreugeri* was collected, are identical with those of "*Hipparion*" *hippidiodus* from Qiangyang. Whether one chooses to refer "*Hipparion*" *kreugeri* to "*Hipparion*" *hippidiodus,* or to accept some potential affinities with "*Hipparion*" *platyodus,* it is clear that the advanced stage of cheek tooth wear and the poor state of preservation of this specimen makes its referral to any taxon questionable, and its recognition as a distinct species untenable. We believe that "*Hipparion*" *kreugeri* is best considered a nomen dubium.

TABLE 5
Measurements on Chinese Hipparionine Mandibles[a]

Specimen No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14
"*Hipparion*" *platyodus*														
(1) PMU M3691		93.7	77.5	69.0	146.0		46.0					41.8	79.5	29.8
(2) AMNH 91 B979		110.3	69.8	64.5	134.3	81.5				93.1	68.0	54.0		
"*Hipparion*" *dermatorhinum*														
(3) AMNH 41 L310		105.8	78.6				44.5			98.0	69.4	44.5	75.9	25.6
"*Hipparion*" *forstenae*														
(4) AMNH 41 L333	293.2	85.5	85.9			74.1	38.7	129.5	124.0	57.9	53.5	37.9	56.7	35.0
Proboscidipparion sinense														
(5) PMU M3925	470.0	126.8	88.1	81.7	171.6	134.1	57.4	215.5	206.0	108.3	87.3	66.4	103.8	36.0

[a] Measurements 1–14 as given in figure 3.

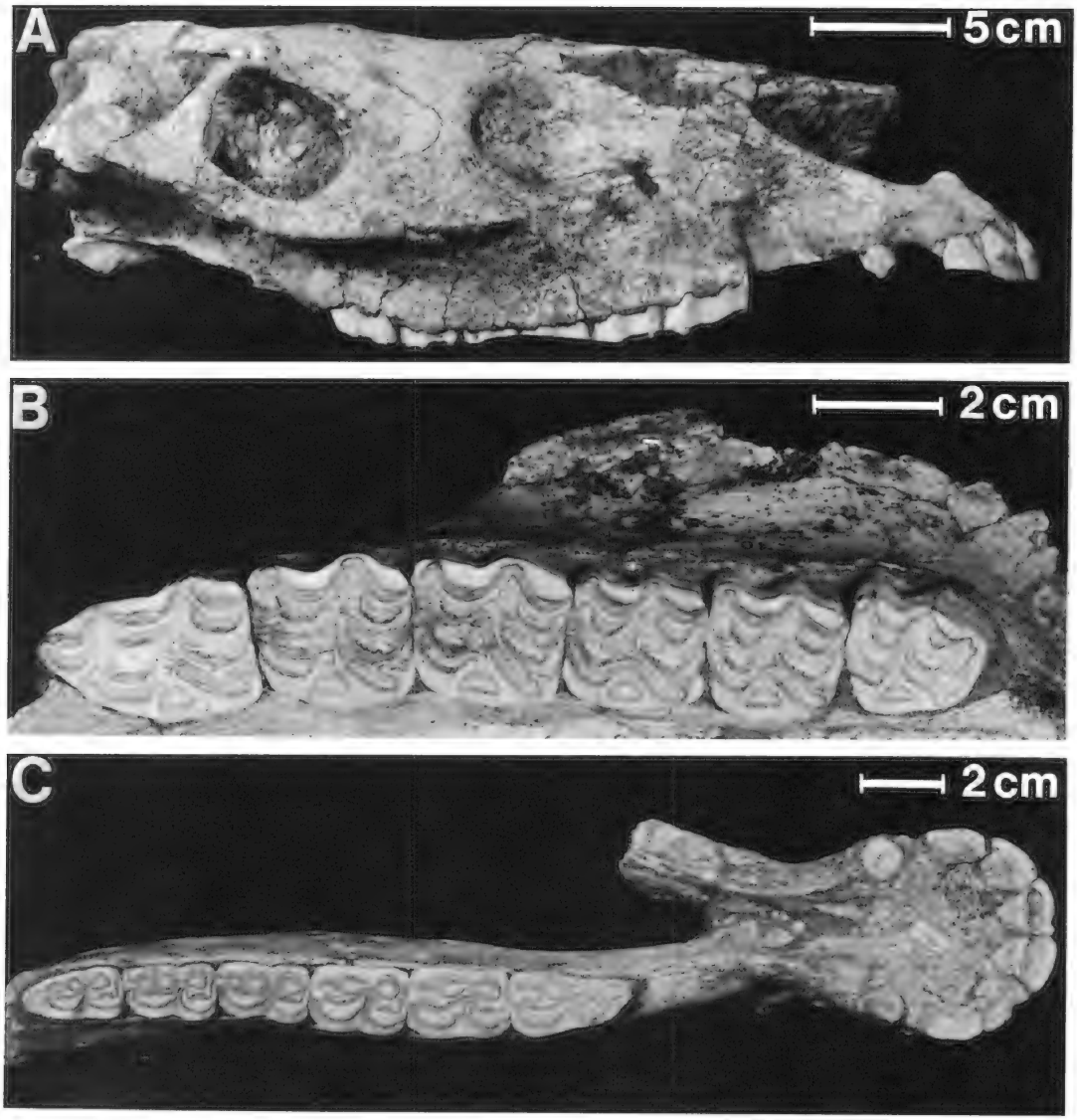

Fig. 4. "*Hipparion*" *platyodus,* PMU M3691 (lectotype), from Locality 70, Wuxiang County, Shanxi Province, late Miocene. **A.** Right lateral view of skull. **B.** Left occlusal view of cheek teeth. **C.** Dorsal view of mandible.

Morphologically, "*H.*" *platyodus* closely resembles "*H.*" *weihoense* (Liu et al., 1978) which, in turn, appears quite similar to "*Hipparion*" *primigenium* (s.s.). "*H.*" *weihoense* and "*H.*" *platyodus* are both advanced compared to "*H.*" *primigenium* in having a preorbital fossa orientation that is rotated slightly dorsally. "*H.*" *platyodus* would appear to be derived compared to "*H.*" *weihoense* in its reduced dimensions, posterior pocketing, medial depth and peripheral outline of the POF. However, it is similar in overall size, nasal notch incisure, and cheek tooth morphology. "*H.*" *platyodus* is derived compared to "*H.*" *primigenium* (Bernor et al., in prep.) in having a somewhat shortened snout, metaconids and metastylids with angular, rather than rounded opposing borders, and a tendency for the molars to develop deeply incised and broadly U-shaped linguaflexids. These lower cheek tooth character states are potentially shared with "*Cormo-*

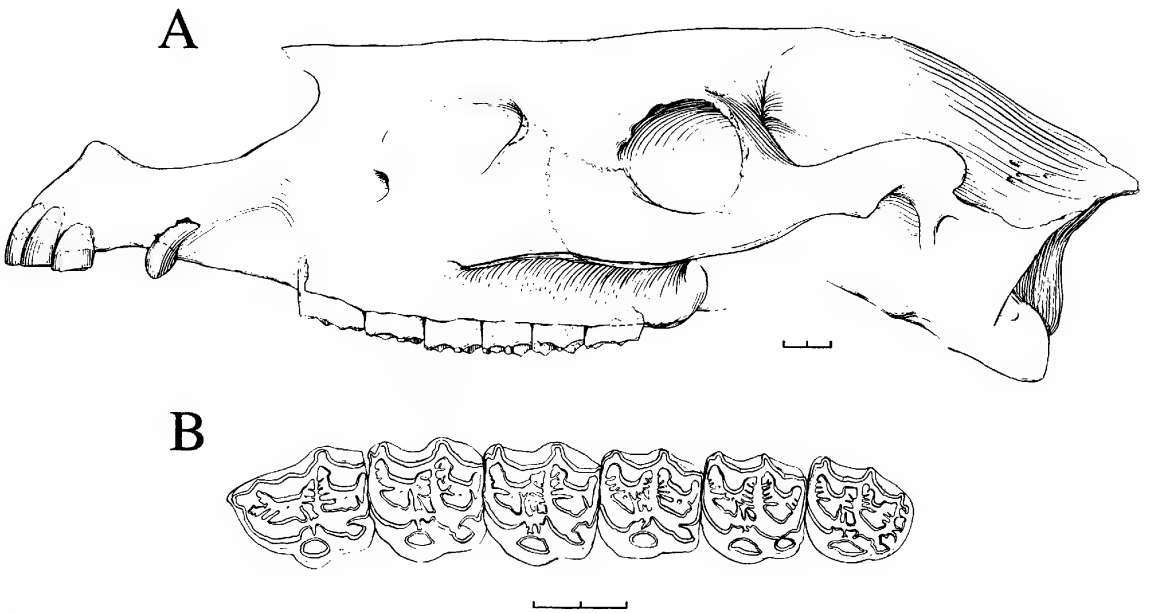

Fig. 5. "*Hipparion*" cf. *platyodus*, AMNH 91 B979. **A.** Left lateral view of skull. **B.** Left occlusal view of cheek teeth.

hipparion" (*Sivalhippus*) *perimense* (sensu Bernor and Hussain, 1985) and "*H.*" *houfenense* of Chinese Jinglean and early Nihowan age (= Pliocene; Flynn and Bernor, 1987). Citing principally lower cheek tooth characters, Bernor et al. (in press) have suggested that "*H.*" *platyodus* is a primitive member of their "*Sivalhippus*" Complex, and have provisionally referred this species to "*Sivalhippus*" *platyodus*.

"*Hipparion*" *coelophyes* Sefve, 1927

Hipparion fossatum Sefve, 1927: 26, pl. IV, fig. 13.
Hipparion coelophyes Sefve, 1927: 29, pl. V, figs. 16–18.
Hipparion parvum Sefve, sensu Hu Changkang, 1962.
Hipparion plocodus Sefve, sensu Forsten, 1968, in part.
Hipparion plocodus Sefve, sensu Zhegallo, 1978, in part.
Hipparion (*Hipparion*) *coelophyes* Sefve, sensu Qiu et al., 1987.

LECTOTYPE: PMU M3688.

LECTOTYPE LOCALITY: Locality 44, Baode County, Shanxi Province, China (Zdansky, 1923).

LOCALITIES: PMU M3690 and M311—Locality 44; PMU M309, M3689, M594 and M590—Locality 43; PMU M584—Locality 109 (Zdansky, 1923), all Baode County, Shanxi Province.

AGE: Late Miocene.

REFERRED SPECIMENS: PMU M3690, skull; M311, skull. "*H.*" aff. *coelophyes*: M309, skull; M3689, skull fragment; M584, skull fragment. "*H.*" ?*coelophyes*: M594, palate fragment; M590, palate fragment.

GEOGRAPHIC RANGE: Qingyang, Gansu; Baode, Shanxi; Huade, Nei Mongol, China.

DIAGNOSIS: Medium- to small size hipparionine species; POB relatively long (in "*Hipparion*" *coelophyes* s.s. = 42.2–46.2 mm); lacrimal placed posterior to POF; POF slightly developed, varying from egg- to C-shaped in outline, posterior pocketing slight to absent, medial depth moderate to very shallow, peripheral border outline moderate to weak; nasal notch generally at anterior border of P2; snout elongate and slender; cheek tooth row length 125.5–140.1 mm, with complex fossette plications, pli caballins bifid, hypoglyphs deeply incised, protocones labially rounded and lingually flattened.

DESCRIPTION: We refer three PMU specimens to "*Hipparion*" *coelophyes* (s.s.): M3688 (lectotype), an old adult female (figs. 6 and

8A), virtually complete except for the posterior cranium, zygomatics, and right M2–3; M3690, a nearly complete adult female skull (figs. 7 and 8B) lacking incisor region, right canine, and posterior cranium, but with the rest of the snout, right and left P2–M3; M311 (fig. 8C), an adult skull, complete except for the anterior dentition, lingual borders of right P2–3, right anterior and inferior orbital rim, left orbit and zygomatic arch. In addition, we refer another three specimens to "*Hipparion*" aff. *coelophyes*: M309 (fig. 8D), a nearly complete subadult female skull lacking the anterosuperior portion of the maxilla, left orbit, right posterior orbit, most of the cranium, both I1s and canine crowns; M3689 (fig. 8E), an adult skull fragment lacking cranium, posterior orbits, premaxilla and anterior dentition, right and left P2, and the buccal borders of P2–3; M584 (fig. 8F), a complete adult skull, lacking only the canines, left I3, anteriormost portion of the nasals, and the posterior cranium. We also refer two remaining specimens to "*Hipparion*" ?*coelophyes*: PMU M594, an adult palate fragment with right P4–M3 and left P3–M3; M590, an adult palate fragment with right P2–M2 and left P2–M1.

PMU M3688 is a medium-size hipparionine with an elongate and slender snout. The preorbital bar is long for the size of this individual, and the anteriormost extent of the lacrimal is placed posterior to the preorbital fossa. The preorbital fossa is anteroposteriorly oriented, has an elongate egg shape, is not posteriorly pocketed but has a posterior rim, is medially shallow, with a faint anterior rim, and weak peripheral border outline. The nasal notch is retracted just to P2 anterostyle. The incisors are heavily worn but retain small, circular and centrally placed infundibula. The canines are small and peg-shaped, lacking enamel caps on their apices. The cheek teeth are in an advanced stage of wear so that the fossettes are only simply (P2) to moderately (P3–M3) complex. Pli caballins are single on P3–4 and bifid on M1–3. Hypoglyphs are moderately deep on P2, and deep on the remaining cheek teeth. The protocone is lingually flattened and labially rounded on all cheek teeth except M3, on which it is elongate. P2 has an elongate anterostyle.

PMU M3690 has a long preorbital bar; the lacrimal suture approaches but does not touch the posterior rim of the preorbital fossa. The fossa is only a little greater in its dorsoventral dimension than the fossa ventral border–facial maxillary crest dimension. It is egg-shaped and anteroposteriorly oriented, has a moderate medial depth, and lacks posterior pocketing, but it has a posterior rim, and the anterior rim is faint, while the fossa peripheral border outline is moderately strong. The buccinator fossa is distinct and well developed. The nasal notch is slightly more incised than in the lectotype, extending to a level above anteriormost P2. The cheek teeth are complexly plicated. Pli caballins are bifid on all cheek teeth except M2. Hypoglyphs are deeply incised on all cheek teeth except M3, on which they are very deeply incised. The protocones are lingually flattened and labially rounded on all cheek teeth. P2 is as in the lectotype specimen.

PMU M311 is similar to the lectotype in its morphology. In details of the preorbital bar and facial fossa complex it differs from PMU M3688 only in its slightly greater fossa medial depth (perhaps due to vertical crushing), more prominent anterior rim, and more strongly expressed fossa peripheral outline. The cheek teeth are in an early, approximately middle adult, stage of wear. Plications of the pre- and postfossettes are complex. Pli caballins are bifid and hypoglyphs are deeply incised on all cheek teeth. Protocones are lingually flattened and labially rounded. P2 has an elongate anterostyle. In middle adult wear, M311 would have had its cheek tooth morphology virtually identical to that of the lectotype specimen.

PMU M309 is similar to the abovementioned three specimens in its size and snout morphology. The preorbital bar is only negligibly shorter, but the lacrimal is identical in its morphology. The preorbital fossa differs from the above-described specimens in its fainter expression. As with the three previous specimens, there is no posterior pocketing, but a posterior rim. Preorbital fossa medial depth is shallow, anterior rim is absent, and the peripheral border outline dissipates ventrally and anteriorly, with no apparent anterior rim. The buccinator fossa is shallow. The I1s are missing but I2–3 have elongate infundibula. The canines are broken, but their

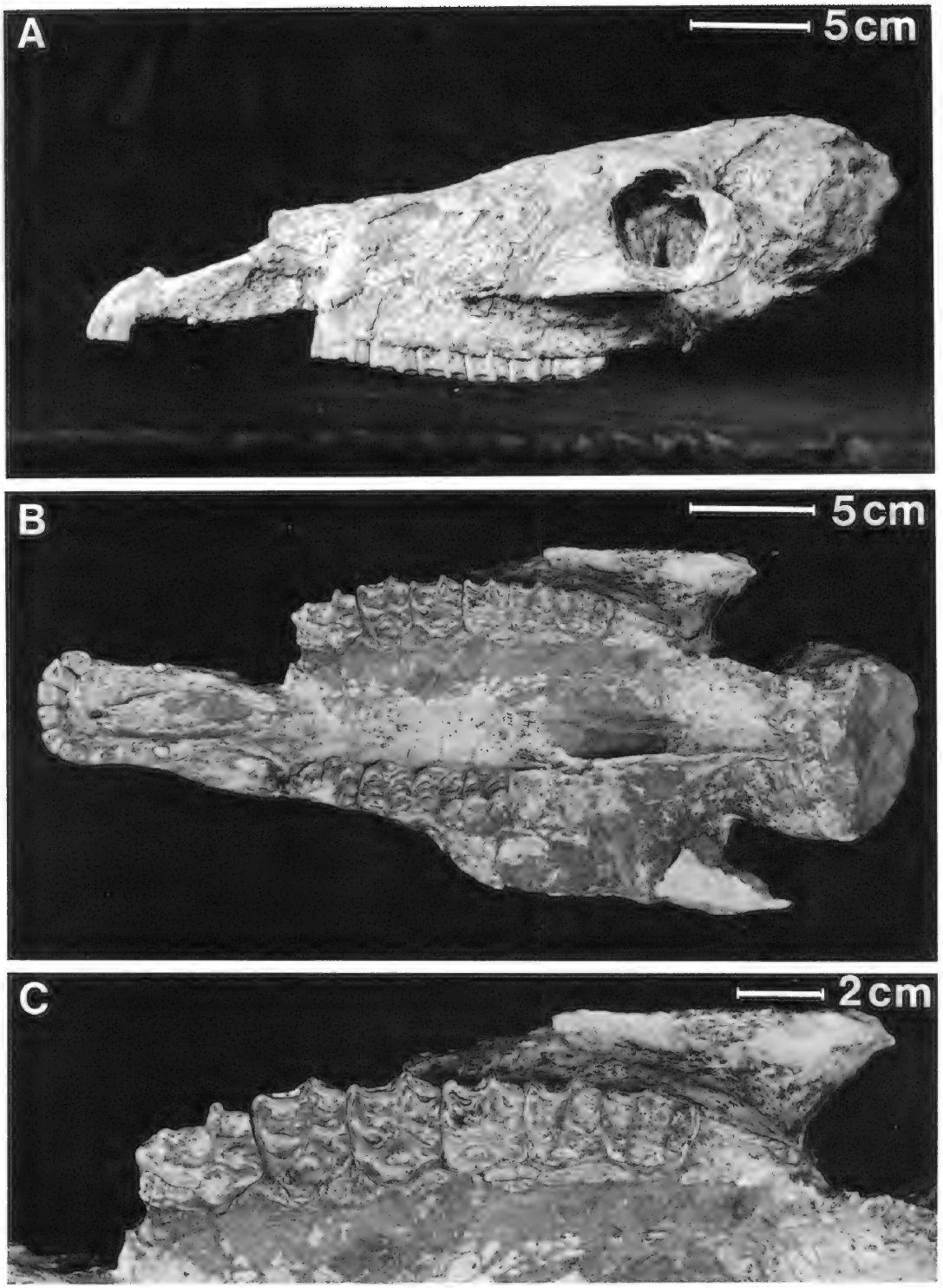

Fig. 6. "*Hipparion*" *coelophyes*, PMU M3688 (lectotype), from Locality 44, Baode County, Shanxi Province, late Miocene. **A.** Left lateral view of skull. **B.** Ventral view of skull. **C.** Left occlusal view of cheek teeth.

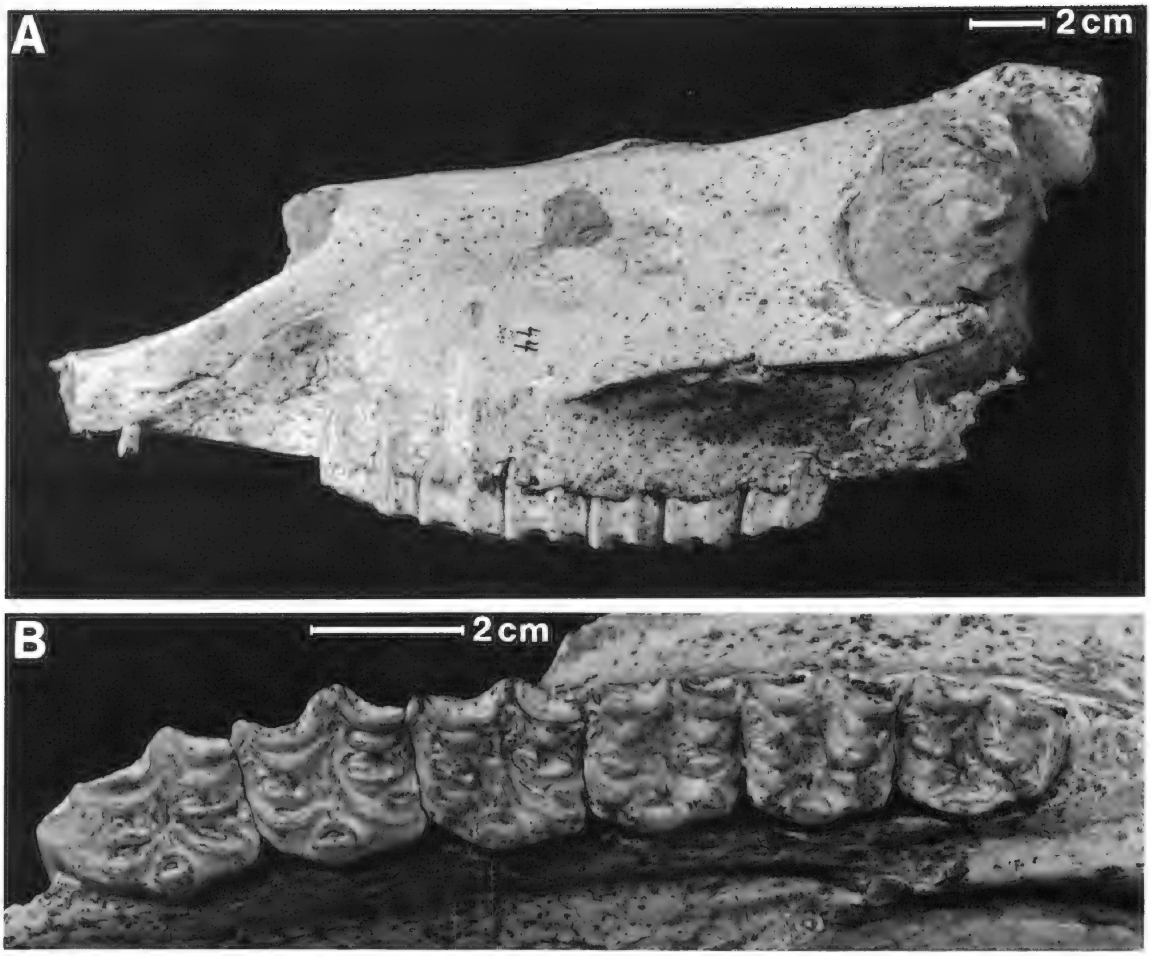

Fig. 7. "*Hipparion*" *coelophyes,* PMU M3690, from Locality 44, Baode County, Shanxi Province, late Miocene. **A.** Left lateral view of skull. **B.** Left occlusal view of cheek teeth.

alveoli show small roots. The premolars have moderately complex plications of the pre- and postfossettes, while the molars are quite complex; M3 is not yet completely erupted and has not yet worn so as to show its morphology. Pli caballins are bifid or complex on all cheek teeth. Hypoglyphs are deeply to very deeply incised on all cheek teeth except P3 which is somewhat more shallowly incised. The protocone is lingually flattened on P3–M2 and more elongate on P2. P2 anterostyle is elongate and buccolingually compressed.

PMU M3689 has a preorbital bar which is only faintly delimited. The preorbital fossa is vestigial, there is only a faint medial depression, and the peripheral border and anterior rim are absent. The cheek teeth are in an advanced stage of wear but all still show considerable complexity as in PMU M309. Pli caballins are single on the premolars, bifid on the molars. Hypoglyphs are increasingly more deeply incised serially from P3–M3, and would have probably been deeply to moderately deeply incised in middle adult wear. The protocones remain distinctly flattened lingually and rounded labially despite their advanced wear, except m3 which is elongate.

As with PMU M3689, PMU M584 shows a reduced expression of the preorbital fossa. Yet in size, snout proportions, and cheek tooth morphology, it is similar to the rest of the hypodigm of "*H.*" *coelophyes.* The preorbital fossa is virtually absent except for a faint posterior rim and medial depression. Accompanying this reduction is a concomitant reduction in the preorbital bar length. Also, the

peripheral border outline is weaker, dissipating ventrally and anteriorly. The anterior rim is distinct. The preorbital fossa medial wall, intermediate and buccinator fossae are as in all the abovementioned specimens. This individual's cheek teeth are approximately in a middle adult stage of wear. The pre- and postfossettes are moderately complex on P4–M3, simple on P2–3. Pli caballins are bifid on all cheek teeth. Hypoglyphs are moderately deeply incised on P2–4, and progressively more deeply incised in the molar series. Protocones show a degree of lingual flattening on the cheek teeth. P2 anterostyle is elongate.

The two specimens referred here to "*Hipparion*" ?*coelophyes,* PMU M594 and M590, are palate fragments retaining cheek tooth morphology but no facial morphology. These specimens agree well with "*Hipparion*" *coelophyes* (s.l.) in size as well as various cheek tooth characters. They both show moderate complexity of the pre- and postfossettes, hypoglyphs are generally deeply incised and the protocones are either lingually flattened and labially rounded or elongate. Whereas PMU M594 has persistently bifid or complex pli caballins, PMU M590 is variable, showing a predominantly single pli caballin morphology. In this regard, this specimen shows greater similarity to "*H.*" aff. *coelophyes.* PMU M590 has left P2 hypocone encircled by an enamel band.

DISCUSSION: The taxonomy of "*H.*" *coelophyes* is problematical. Qiu et al. (1987) originally formally recognized "*H.*" *fossatum* as a valid taxon because PMU M3690 had page and figure number priority over PMU M3688, the lectotype of *H. coelophyes* (sensu Sefve, 1927), and because PMU M3690 is better preserved and has cheek teeth which are not so worn as PMU M3688. However, Forsten (1985: 123) proposed as the lectotype of *H. fossatum,* a very enigmatic specimen, PMU M3821 A + B (Sefve, 1927: Taf. IV, figs. 14 and 15), a coronally sectioned skull and associated lower jaw with highly worn cheek teeth. This specimen is quite different from one of two other specimens which Sefve figured and implicitly referred to *H. fossatum,* PMU M3690 (Sefve, 1927: Taf. IV, fig. 13), and our entire hypodigm of *H. coelophyes.* The third specimen referred by Sefve to *H. fossatum* is a premaxilla and anteriormost maxillary fragment which is too incomplete to be determined as any specific taxon. In all actuality, PMU M3821 A + B cannot be referred with certainty to any bonafide taxon because of its very advanced stage of cheek tooth wear, highly reduced facial fossa, and lack of nasal bone area. We find Forsten's use of PMU M3821 A + B as a lectotype of *H. fossatum,* or any other species for that matter, inappropriate, and therefore believe that the taxon is best considered a nomen dubium. We discuss this specimen's morphological resemblances to "*H.*" *forstenae* later in the discussion of that taxon. It should be noted however that otherwise Forsten's (1985) hypodigm of "*H.*" *fossatum* conforms closely with ours of "*H.*" *forstenae* (= *H. richthofeni* of Sefve, 1927).

The entire referred assemblage of "*Hipparion*" *coelophyes* is heterogeneous in preorbital fossa morphology and, to a lesser extent, cheek tooth morphology. However, specimens from Locality 44, which we refer to "*H.*" *coelophyes* s.s. are homogeneous in their morphology. Their lacrimals are placed distinctly posterior to the preorbital fossa; the fossae have an elongate egg shape and are anteroposteriorly oriented; their medial depth is usually moderate as is the peripheral border outline. The cheek teeth are virtually always complexly plicated, pli caballins are double, hypoglyphs are deeply incised and protocones are lingually flattened and labially rounded.

The two Locality 43 specimens referred here to "*Hipparion*" aff. *coelophyes,* PMU M309 and M3689, show marked preorbital fossa reduction; the preorbital bar and the posterior fossa rim are vestigial, and medial depth is shallow to absent. The cheek teeth retain mostly the same morphology as the Locality 44 specimens but show a tendency to occasionally have single pli caballins and less deeply incised hypoglyphs. The single Locality 109 specimen, M584, has a preorbital fossa morphology similar to the two Locality 43 specimens, but shows decreased complexity of the pre- and postfossette plications and more elongate protocones.

In the variety of facial and cheek tooth characters cited here, the hypodigm of "*H.*" *coelophyes* would appear to be morphologi-

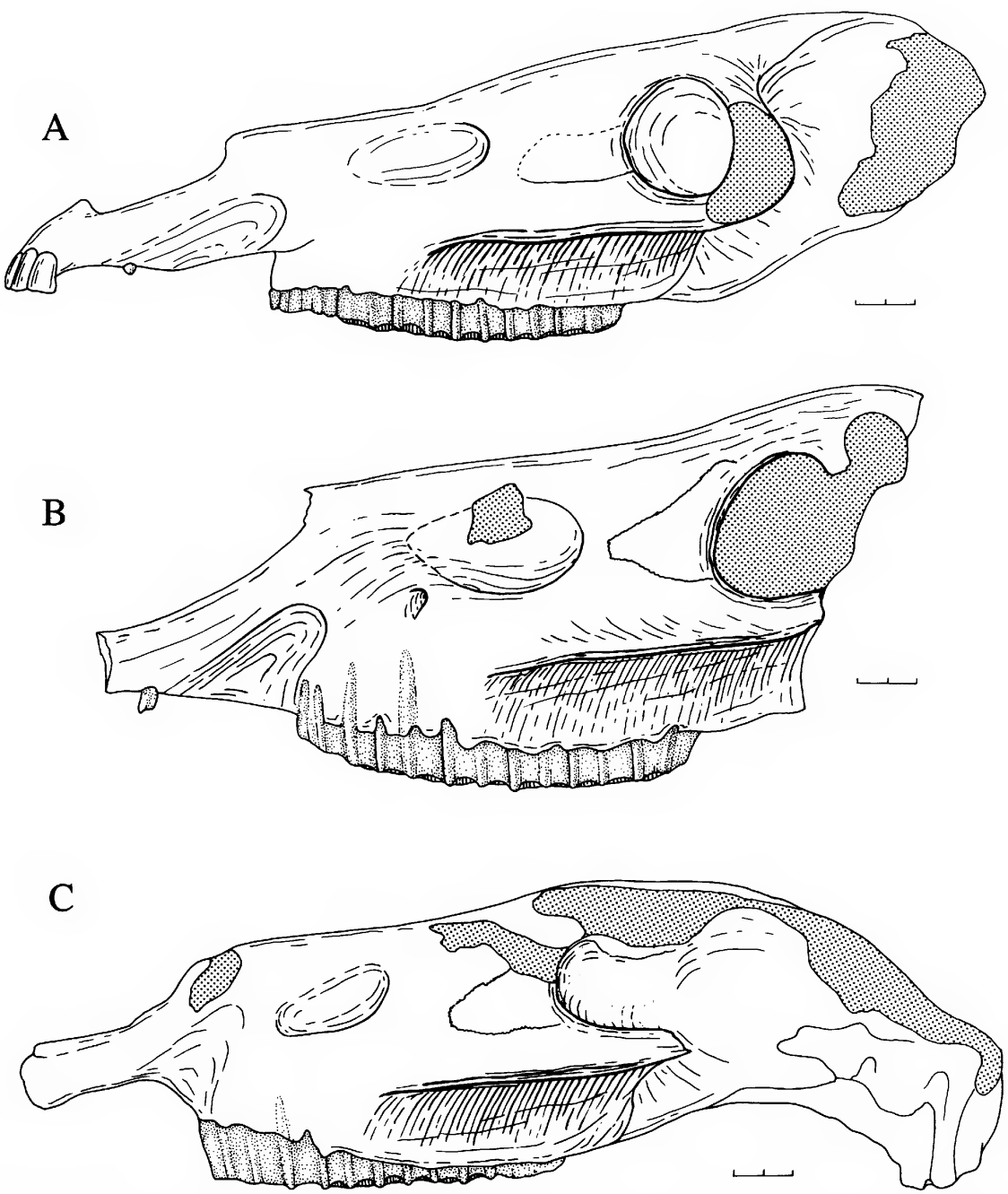

Fig. 8. Specimens referable to "*Hipparion*" *coelophyes,* left lateral view of skulls. **A.** PMU M3688 (lectotype, also fig. 6). **B.** PMU M3690 (also fig. 7), Locality 44. **C.** PMU M311, Locality 44. **D.** PMU M309, Locality 43. **E.** PMU M3689 (reversed), Locality 43. **F.** PMU M584 (reversed), Locality 109.

cally transitional between the more primitive "*H.*" *platyodus* and "*H.*" *hippidiodus.* In its facial morphology "*H.*" *coelophyes* s.l. shows a reduced expression of several preorbital fossa complex character states and there is a tendency to have a slightly incised nasal notch. The cheek teeth appear to be somewhat less complex in pre- and postfossette plications, there is a tendency to occasionally have single pli caballins, hypoglyphs are less deeply incised, especially in later stages of wear, and protocones lose their lingual flattening, be-

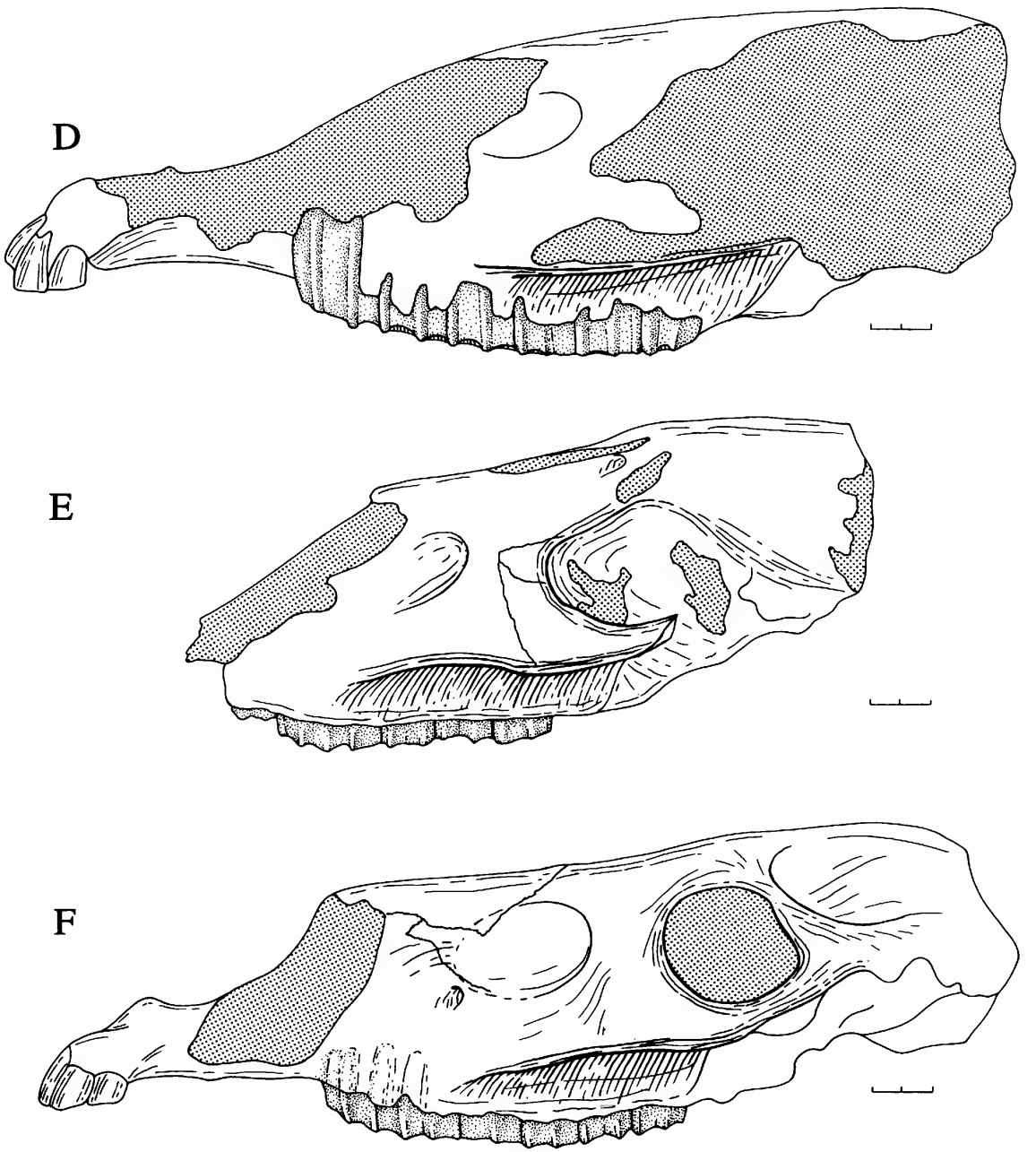

Fig. 8.—*Continued*

come more elongate, and eventually rounded.

"*Hipparion*" *hippidiodus*
Sefve, 1927

Hipparion richthofeni Koken, sensu Teilhard de Chardin, 1922.
Hipparion hippidiodus Sefve, 1927: 9, table I, fig. 4, pl. IV, fig. 12.

LECTOTYPE: PMU M3819.

LECTOTYPE LOCALITY: Locality 115, Qingyang County, Gansu Province (Zdansky, 1923).

LOCALITIES: PMU M3819, M252, Locality 115; PMU M248, M249, M250, M251, M595, M596, Locality 43; PMU M247, Locality 44; PMU M253, Locality 52.

AGE: Late Miocene.

REFERRED SPECIMENS: PMU M249, M596, M595, M247, and M248, skull fragments; M250, left palate fragment; M3818, anterior skull fragment; M251, left palate fragment; M252, right palate fragment; M253, palate fragment.

GEOGRAPHIC RANGE: Qingyang, Gansu; Baode, Shanxi; western part of the Mongolian People's Republic; ?Kazakhstan, U.S.S.R.

DIAGNOSIS: Medium-size hipparion; POF shallow to absent; maxillary cheek tooth series 147.9 mm in length, with moderate to simple fossette plications, pli caballins usually single, hypoglyphs moderately deeply incised, protocone slightly elongate to rounded.

DESCRIPTION: Eleven skull fragments are referable to "*Hipparion*" *hippidiodus*: PMU M3819 (figs. 9 and 10A), an old adult skull fragment with all cheek teeth, but lacking posterior portion of the orbits, cranium, nasals, and snout; PMU M249 (fig. 10B), an adult skull fragment with left P2–4 and right P3–M2, lacking orbits, cranium, nasals, and snout; PMU M596 (fig. 10C), an adult skull fragment with right and left M1–3, lacking premolars, snout, nasals, orbits, and cranium; PMU M595 (fig. 10D), a juvenile skull fragment with right and left dP4 and M1–2, lacking cranium, nasals, anterior palate, and snout; PMU M247, an adult palate fragment with right and left P3–M2; PMU M248, an adult palate fragment with fragmentary right P3 and P4–M2; PMU M250, a juvenile left palate fragment with dP2–4; PMU M3818, an adult maxillary and premaxillary fragment containing right I2–3, canine root and P2–3, and left I3, C, and P2–3 (the skull is missing posterior to P3 on each side); PMU M251, a left juvenile maxillary fragment with dP1–4; PMU M252, an old adult P2–M1 series; PMU M253, a juvenile palate with P1–M2.

The lectotype, PMU M3819, has only a very shallow, concave depression for a preorbital fossa, lacking any orientation, pocketing, anterior rim, or peripheral border; traces of a preorbital bar have all but disappeared. Neither the area of the buccinator fossa nor the nasal notch are preserved. The cheek teeth are uniformly simple in their pre- and postfossette plication complexity. Pli caballins are shortened and essentially single. Hypoglyphs are moderately deeply incised on P3–M2, shallow on P2 and deep on M3. Protocones are round on all cheek teeth except M3, where they are elongate.

PMU M249 is similar to the lectotype in its size and morphology. All features of the preorbital fossa are virtually identical between these two specimens. PMU M249 is a somewhat younger adult and therefore has cheek teeth which are in an earlier stage of wear and still reveal simple pre- and postfossette plication frequencies on the premolars and moderate complexity on the molars. Pli caballins are single and hypoglyphs are moderately deeply incised on all cheek teeth. Protocones are rounded on all cheek teeth except P2, which is only somewhat elongate.

PMU M596 differs from the previous two specimens in that a small, vestigial posterior fossa rim is present. In all other details of the preorbital fossa complex this individual is identical to PMU M249 and M3819. Likewise, the molar pre- and postfossette plications are simple and pli caballins are single. Hypoglyphs are generally moderately incised. All cheek tooth protocones have a rounded-elongate morphology.

PMU M595 has a preorbital fossa morphology virtually identical with that of the lectotype. The dP4 has moderately complex plications of the pre- and postfossettes, the pli caballin is double, the hypoglyph is deeply incised and the protocone is oval. The M1 has a simpler fossette plication frequency, the pli caballin is single, the hypoglyph is deeply incised, and the protocone is elongate. M2 and M3 are still in their crypts, with the former beginning to erupt.

The remaining specimens, PMU M247, M248, M250, M3818, M251, M252, and M253, do not preserve the facial region. Of these specimens, PMU M250 and M251 are the only foals. These two specimens are of similar size, have simple to moderately complex plications of the pre- and postfossettes, variably double or single pli caballins, deeply incised hypoglyphs, and small rounded to somewhat elongate protocones. The remaining specimens have cheek tooth occlusal details similar to the adult material described above.

DISCUSSION: As noted in the previous two systematic sections, "*Hipparion*" *hippidiodus* could be interpreted to represent a terminal segment of the morphoclinal series,

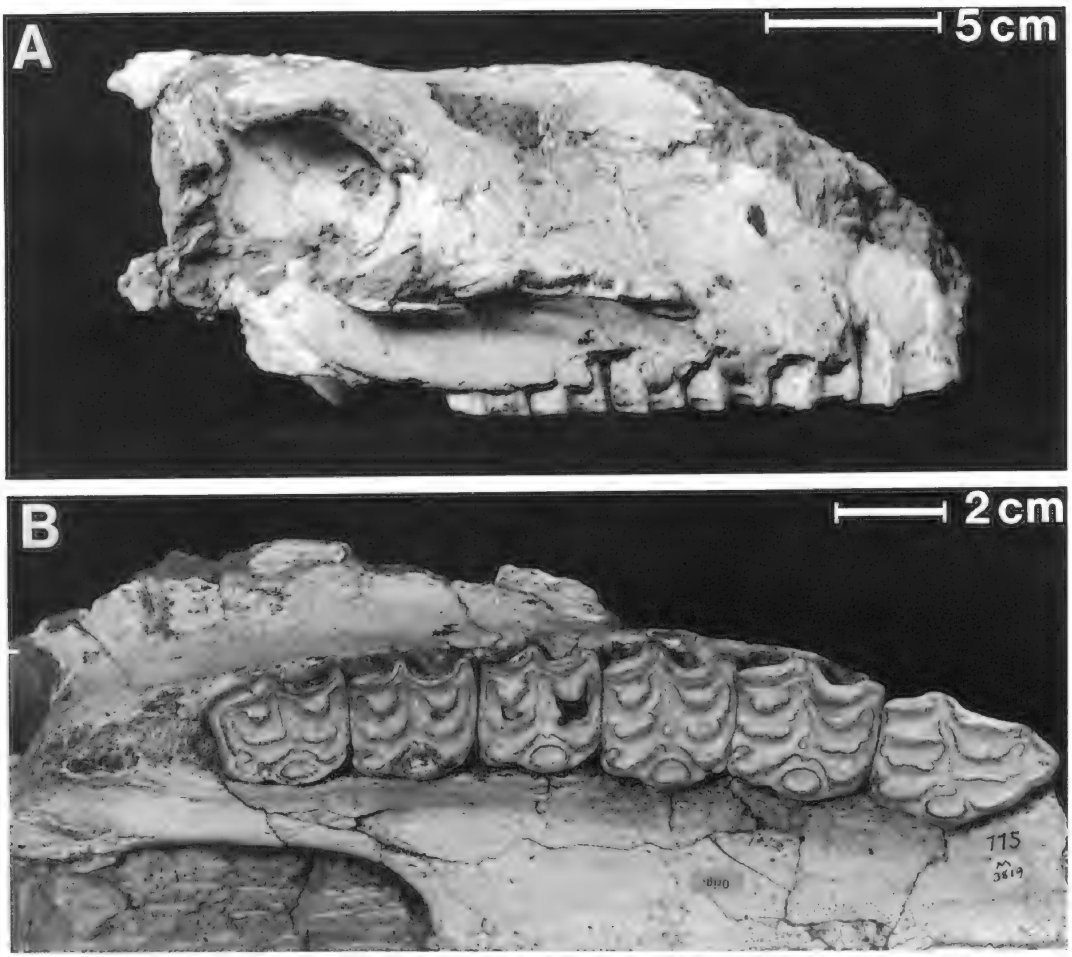

Fig. 9. "*Hipparion*" *hippidiodus,* PMU M3819 (lectotype), from Locality 115, Qingyang County, Gansu Province, late Miocene. **A.** Right lateral view of skull. **B.** Right lateral view of cheek teeth.

"*H.*" *weihoense*–"*H.*" *platyodus*–"*H.*" *coelophyes*–"*H.*" *hippidiodus*. "*H.*" *hippidiodus* is not strictly homogeneous in its morphology. Figure 10 reveals that "*H.*" *hippidiodus* varies somewhat in its facial morphology only in that a vestigial posterior rim may be expressed; otherwise the preorbital fossa is entirely lacking. Cheek tooth morphology includes moderate to simple plication complexity of the pre- and postfossettes, pli caballins that are variably single or double, hypoglyphs that vary from being deeply to shallowly incised, and protocones that vary from being elongate to rounded in their morphology.

"*Hipparion*" *coelophyes* (s.s.) differs consistently from our hypodigm of "*Hipparion*" *hippidiodus* in its better developed preorbital fossa, more complex and thickly banded cheek tooth pre- and postfossette plications, consistently double pli caballins, and lingually flattened and labially rounded protocones. However, specimens referred to here as "*Hipparion*" aff. *coelophyes* reflect a destabilization of these facial and cheek tooth morphologies, and reveal significant preorbital fossa reduction with the preorbital bar becoming vestigial, fossa orientation varying from egg-shaped, to C-shaped, to vestigial, and fossa posterior pocketing being generally more reduced. The cheek teeth of "*H.*" aff. *coelophyes* are relatively variable and show some degree of pre- and postfossette simplification, reduction of pli caballin frequency, less deeply incised hypoglyphs and somewhat more elongate protocones. These states seem

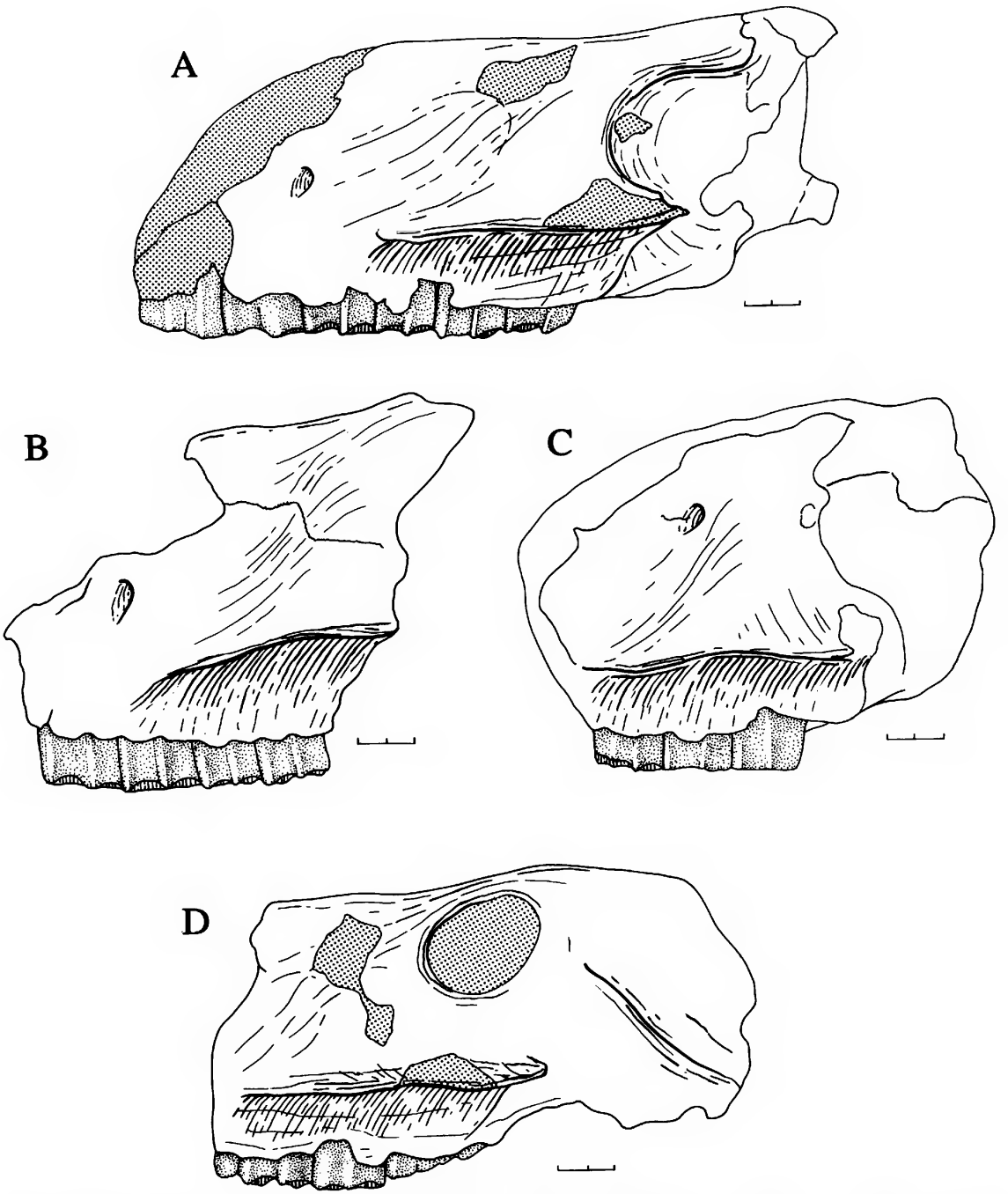

Fig. 10. Specimens referable to "*Hipparion*" *hippidiodus,* left lateral view of skulls. **A.** PMU M3819 (lectotype, reversed; also fig. 8). **B.** PMU M249 (reversed), Locality 43. **C.** PMU M596 (reversed), Locality 43. **D.** PMU M595 (reversed), Locality 43.

to suggest that "*H.*" aff. *coelophyes* and "*H.*" *hippidiodus* may be sister taxa. However, this hypothesis is problematic since "*H.*" *hippidiodus* facial and cheek tooth morphology conform so closely to species of advanced *Hipparion* s.s. (sensu Bernor, 1985), or *Hipparion* (*Hipparion*) sensu Qiu et al. (1987).

The locality data reveal an overlap in oc-

currence of "*H.*" *coelophyes* (s.s.), "*H.*" aff. *coelophyes* and "*H.*" *hippidiodus*. The PMU specimens of "*H.*" *coelophyes* (s.s.) occur only at Locality 44, "*H.*" aff. *coelophyes* at Localities 43 and 109, "*H.*" ?*coelophyes* at Locality 43 and "*H.*" *hippidiodus* at Localities 115 (lectotype locality), 43, 44, and 52. The "*H.*" *hippidiodus* specimen (PMU M249) occurring with "*H.*" *coelophyes* (s.s.) from Locality 44 is strikingly different in its total lack of a preorbital fossa, simplified cheek tooth plications, and rounded protocones. Locality 43 specimens of "*H.*" *hippidiodus* are not so clearly differentiated from "*H.*" aff. *coelophyes,* but do all have more reduced to absent facial fossae and more consistently derived cheek tooth morphologies. The lectotype of "*H.*" *hippidiodus,* from Locality 115, differs convincingly from the lectotype and referred hypodigm of "*H.*" *coelophyes* (s.s.) in its total lack of a facial fossa, more simply plicated cheek teeth, less deeply incised hypoglyphs, and elongate to rounded protocones.

The variability of morphological states seen in specimens which we refer here to "*H.*" *coelophyes* (s.l.) and "*H.*" *hippidiodus* is greater than can be accepted for a single species of hipparionine (based on personal observation by Bernor of the Höwenegg hipparion quarry sample). When considering statistical confidence interval data for "*H.*" *coelophyes* (morphogroup 3) and "*H.*" *hippidiodus* (morphogroup 4), we find that length of the premolar series (variable 7), molar series (variable 8) and entire cheek tooth row (variable 9) is consistently greater in "*Hipparion*" *hippidiodus* (data available in table 1 of computer disc).

Bernor (1985) has reported a similar range of morphological variability in his study of the Maragheh morphoseries "*H.*" *gettyi–H. prostylum–H. campbelli,* where there was a similar transformation from a well-developed preorbital fossa and complex cheek teeth with elongate protocones, to a total lack of a preorbital fossa, and relatively simple cheek teeth with more rounded protocones. However, a significant difference between the Maragheh and this Chinese morphoseries is that there was no known locality/age overlap in the Maragheh series. In the Chinese series, however, there is overlap at the locality level. Qiu (personal observ.) has found that "*H.*" *coelophyes* and *H. hippidiodus* often occur at the same locality. Qiu has also observed that "*H.*" *platyodus,* the species which shows more primitive characters than "*H.*" *coelophyes* and *H. hippidiodus* occurs in later, early Pliocene, localities. These lines of evidence refute a simple notion that the "*H.*" *platyodus–*"*H.*" *coelophyes–*"*H.*" *hippidiodus* morphoclinal series is a chronospecific "gradual" evolutionary lineage. Indeed, as cited above, and in Qiu (1987), "*H.*" *hippidiodus* may not be part of an intra-China evolutionary series, but related to European, western and southern Asian *Hipparion* s.s. (sensu Bernor, 1985).

"*Hipparion*" *ptychodus* Sefve, 1927

Hipparion ptychodus Sefve, 1927: 39.

LECTOTYPE: PMU M347.

LECTOTYPE LOCALITY: Locality 73, Wuxiang County, Shanxi Province, China (Zdansky, 1923).

LOCALITIES: PMU M593 and M350—Locality 114, Ho-chu County, Shanxi Province; PMU M3684—Yushe County, Shanxi Province.

AGE: Late Miocene.

REFERRED SPECIMENS: M3684, skull; PMU M593, skull fragment; M350, skull fragment.

GEOGRAPHIC RANGE: Wuxiang, Yushe and Ho-chu Counties, Shanxi Province; ?Henan Province; China.

DIAGNOSIS: Medium-size hipparion; POB relatively long (44.7–50.2 mm in adult individuals); anteriormost limit of lacrimal placed well posterior to POF; POF placed anterodorsally on face, anteroposteriorly oriented, posterior pocketing slight, medially deep, anterior rim faint, peripheral border moderately expressed; cheek tooth row 134.8–142.2 mm, with very complexly plicated fossettes, pli caballins bifid or complex, hypoglyphs deeply incised, protocones short, lingually flattened and labiallly rounded; P2 anterostyle elongate.

DESCRIPTION: We refer four PMU specimens to "*Hipparion*" *ptychodus*: PMU M347 (lectotype; figs. 11 and 12A), an adult skull with all cheek teeth, lacking the snout, anterior dentition and most of the cranium; M3684 (fig. 12B), a virtually complete adult female skull with right I1–3 and P2–M3, left

I1, I3, and P2–M3, lacking canines, posterior orbits and cranium; M593 (fig. 12C), an old adult individual with right P2–M3, left P3 (fragmentary)–M3, lacking posterior cranium, nasals and snout; M350 (fig. 12D), a juvenile skull fragment with P2–M2, lacking cranium, anterior nasals and snout.

PMU M347 has a very long preorbital bar, and the lacrimal reaches less than half the distance from the orbit to the preorbital fossa. The preorbital fossa is small, dorsoventrally and anteroposteriorly short, and restricted to a position high above the plane of the facial-maxillary crest, and far anterior to the orbit. It is only slightly pocketed posteriorly, its medial depth is great, the anterior rim is faint and the peripheral border outline is moderately well defined. The cheek teeth have very complexly plicated pre- and postfossettes, especially on the molars; pli caballins are bifid, the hypoglyphs are moderately deeply incised and the protocones are relatively short but retain a lingually flattened and labially rounded shape.

PMU M3684 originates from the same locality as the lectotype. It closely resembles the lectotype in its size and morphology. The snout is moderately elongate and robust. The incisors have anteroposteriorly narrow, mesiodistally elongate dentine pools. The canines are broken, but their roots reveal a small peg-shaped morphology. Morphologically it differs from PMU M347 only in its more reduced preorbital fossa posterior pocketing. The cheek teeth are in a similar stage of wear as the lecotype, and once again reveal a very complex plication amplitude of the fossettes, double pli caballins, moderately deeply incised hypoglyphs, short but lingually flattened protocones, and elongate P2 anterostyles.

PMU M593 is virtually identical to PMU M347 in details of the preorbital fossa complex, except that the preorbital bar is shorter (44.7 versus 50.2 mm). PMU M593 compares well with M3684 in having no posterior pocketing, but merely a posterior rim. Preorbital fossa medial depth is great, but there is only a slightly developed anterior rim. The cheek teeth are heavily worn due to the age of the individual. This has resulted in increased rounding of the protocones, except on M3, which has retained a lingually flattened and labially rounded morphology, and simpler enamel plications.

PMU M350 is a juvenile individual with a somewhat shorter preorbital bar, shallower POF medial depth, and the anterior limit of the lacrimal approaches the posterior rim more closely than in the previously described specimens. Otherwise, the facial morphology is very similar to M347 and M593. The preorbital bar is no shorter than would be expected for this individual's earlier ontogenetic stage of development. The bases of the molar roots partially pierce the ventral floor of the fossa. The cheek teeth reveal a lesser plication complexity of the pre- and postfossettes, possibly due to the very early stage of their wear. The pli caballins are single on P2 and M2, probably due to their early stage of wear, but bifid on P4–M1. Hypoglyphs are deeply incised. Protocones are lingually flattened on P4–M1, and elongate on the remaining cheek teeth, again probably due to the very early stage of wear.

DISCUSSION: Qiu et al. (1987) have recently synonymized this taxon with "*Hipparion*" *platyodus,* citing similarity in size, snout proportions, length of diastema and the lack of nasal notch incision. They further stated that a considerable range of variability in preorbital fossa morphology must be accepted if "*Hipparion*" *ptychodus* is included within "*Hipparion*" *platyodus.*

Bernor et al. (in press) believe that "*H.*" *ptychodus* is unique compared to other Chinese hipparionines in its placement of the facial fossa far anteriorly and high dorsally above the plane of the facial-maxillary crest, and believe that this marks its relationship with the "*Sivalhippus*" Complex. This assertion is further supported by our statistical analysis (e.g., table 5, var. 32). The lectotype and PMU M3684 are in a middle adult stage of wear, revealing more complex and thinly banded plications of the pre- and postfossettes than is known for the other taxa recognized here.

"*H.*" *ptychodus* resembles the Siwalik species, "*Cormohipparion*" (*Sivalhippus*) *perimense* (Bernor and Hussain, 1985: fig. 16) in the anterodorsal placement and shape of the preorbital fossa. Comparison of table 4 here with table 6 of Bernor and Hussain (1985) reveals that the preorbital bar is somewhat

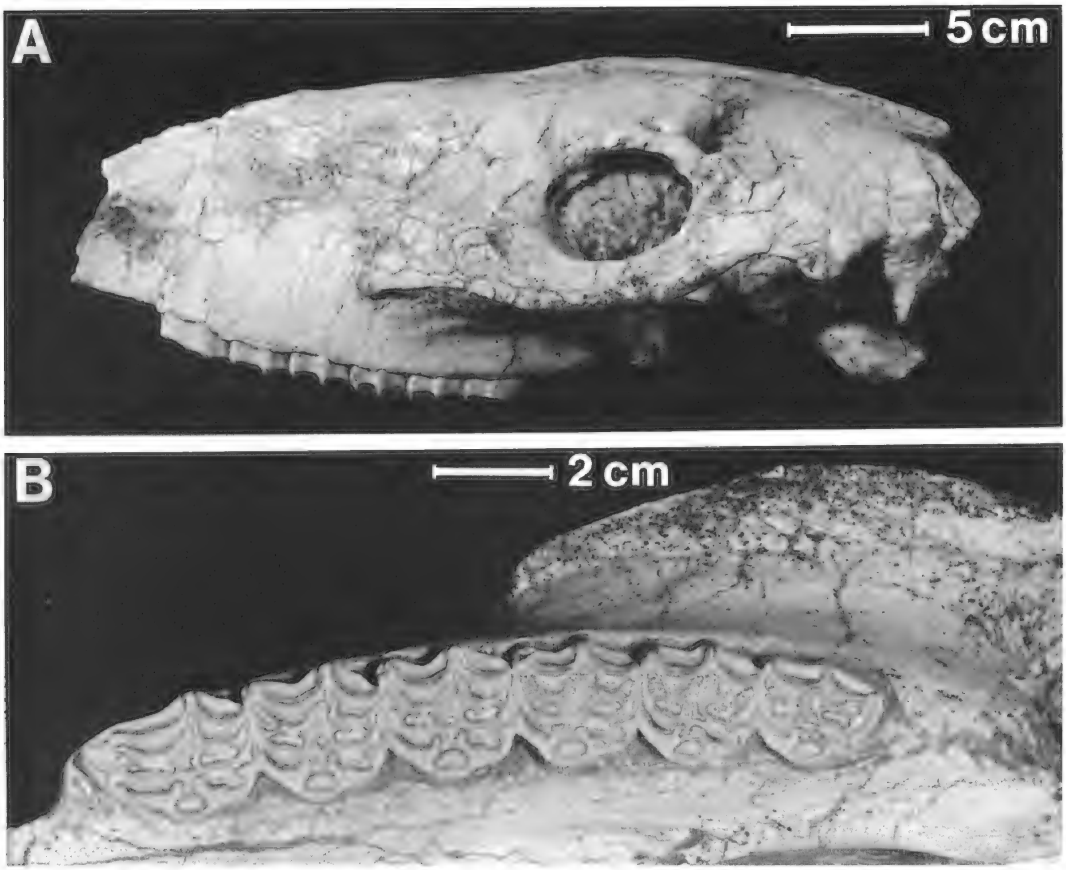

Fig. 11. "*Hipparion*" *ptychodus,* PMU M347 (lectotype), from Locality 73, Wuxiang County, Shanxi Province, late Miocene. **A.** Left lateral view of skull. **B.** Left lateral view of cheek teeth.

shorter in "*H.*" *ptychodus* than "*C.*" (*S.*) *perimense,* while the fossa is consistently longer in the former than the latter species. However, there is a complete overlap between the two species in dorsoventral height and facial-maxillary crest measurements. "*H.*" *ptychodus* also differs from "*C.*" (*S.*) *perimense* in cheek tooth morphology, having somewhat shorter protocones and more thinly banded and complexly plicated pre- and postfossettes.

Both "*H.*" *ptychodus* and "*C.*" (*S.*) *perimense* have derived facial morphologies compared to "*H.*" *weihoense.* The greater length preorbital bar and lesser anteroposterior fossa dimensions of "*C.*" (*S.*) *perimense* suggest its greater stage of derivation in preorbital fossa morphology. However, "*H.*" *ptychodus* would appear to be more strongly divergent from "*H.*" *weihoense* than "*C.*" (*S.*) *perimense* is in its highly complex and more thinly banded pre- and postfossette plications, often complex pli caballins, and apparently shorter protocones. Hence, "*H.*" *ptychodus* and "*C.*" (*S.*) *perimense* appear to share some distinct synapomorphies, whereas "*H.*" *ptychodus* appears also to have autapomorphies which suggest that these two species diverged early in the evolution of the "*Sivalhippus*" Complex (sensu Bernor et al., in press). This evolutionary pattern, if verified, would be consistent with a vicariant model of speciation.

"*Hipparion*" *dermatorhinum* Sefve, 1927

Hipparion dermatorhinum Sefve, 1927: 13, pl. 1, figs. 1–3.

LECTOTYPE: PMU M3872.

LECTOTYPE LOCALITY: Locality 30, Baode

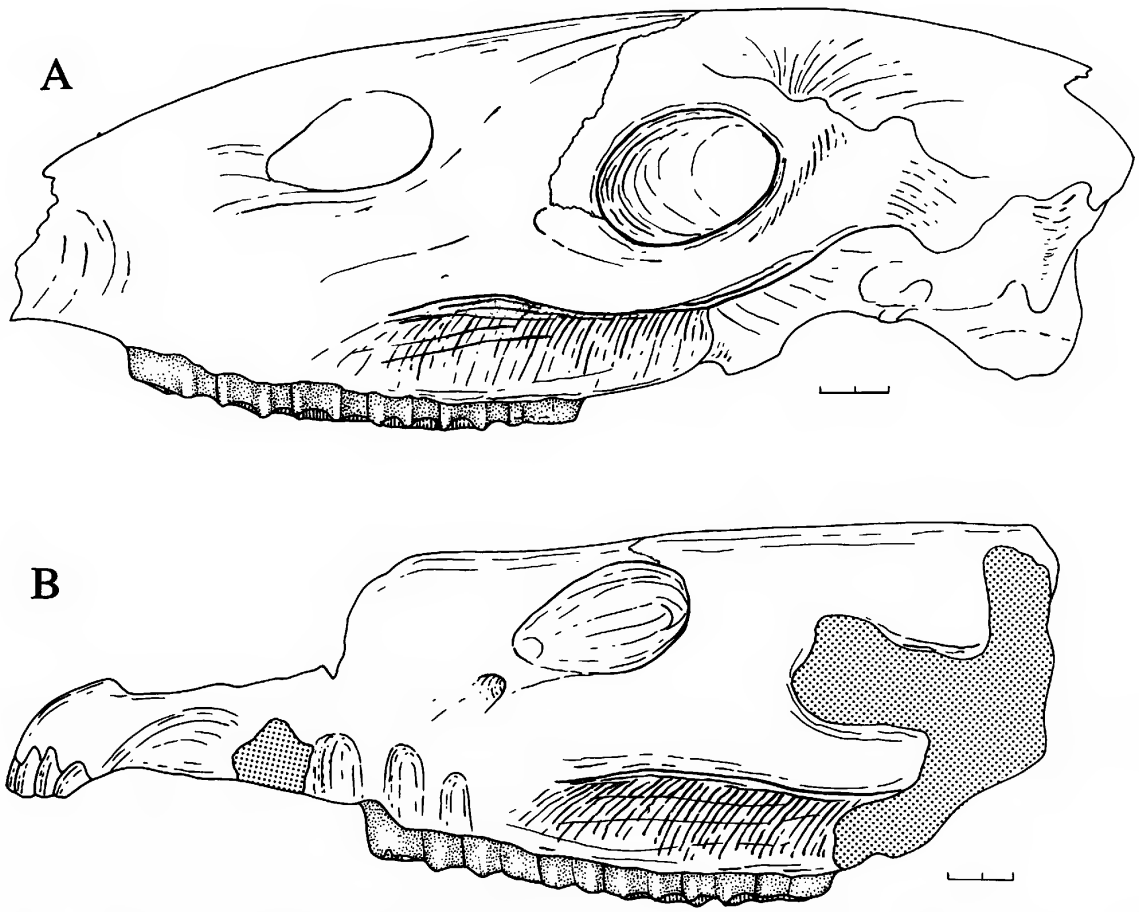

Fig. 12. Specimens referable to "*Hipparion*" *ptychodus,* left lateral views of skulls. **A.** PMU M347 (lectotype, also fig. 11). **B.** PMU M3684 (reversed), Locality 73. **C.** PMU M593 (reversed), Locality 114. **D.** PMU M350, Locality 114.

County, Shanxi Province, China (Zdansky, 1923).

LOCALITIES: PMU M260, Locality 110; PMU M258/M259, Locality 51; PMU M261, Locality 30; AMNH 41-L310, Locality 109.

AGE: Late Miocene.

REFERRED SPECIMENS: PMU M260, skull fragment; PMU M258/M259, left palate fragment; PMU M261, palate fragment; AMNH 41-L310, skull with associated mandible.

GEOGRAPHIC RANGE: Baode, Shanxi Province, China.

DIAGNOSIS: Large hipparion; POB moderately long (37.3–43.6 mm); lacrimal placed posterior to POF; snout elongate, tapering anteriorly to a transversely narrow incisor region; POF subtriangular shaped, anteroventrally oriented, slightly posteriorly pocketed, with moderate medial depth and distinct anterior rim; nasal notch strongly retracted to a position above P4; cheek tooth row 150 mm long with complex fossette plications, pli caballins bifid, hypoglyphs deeply incised, protocones with some lingual flattening and labial rounding; less rounded lingually than labially; mandible with cheek tooth metaconids and metastylids elongate, pli caballinids poorly developed, protostylids present, linguaflexids with shallow U-shape.

DESCRIPTION: Only one specimen in the Uppsala collection, the lectotype PMU M3872 (figs. 13, 14A), is definitely referable to "*Hipparion*" *dermatorhinum.* This is a virtually complete juvenile skull, badly chemically eroded, with all erupted cheek

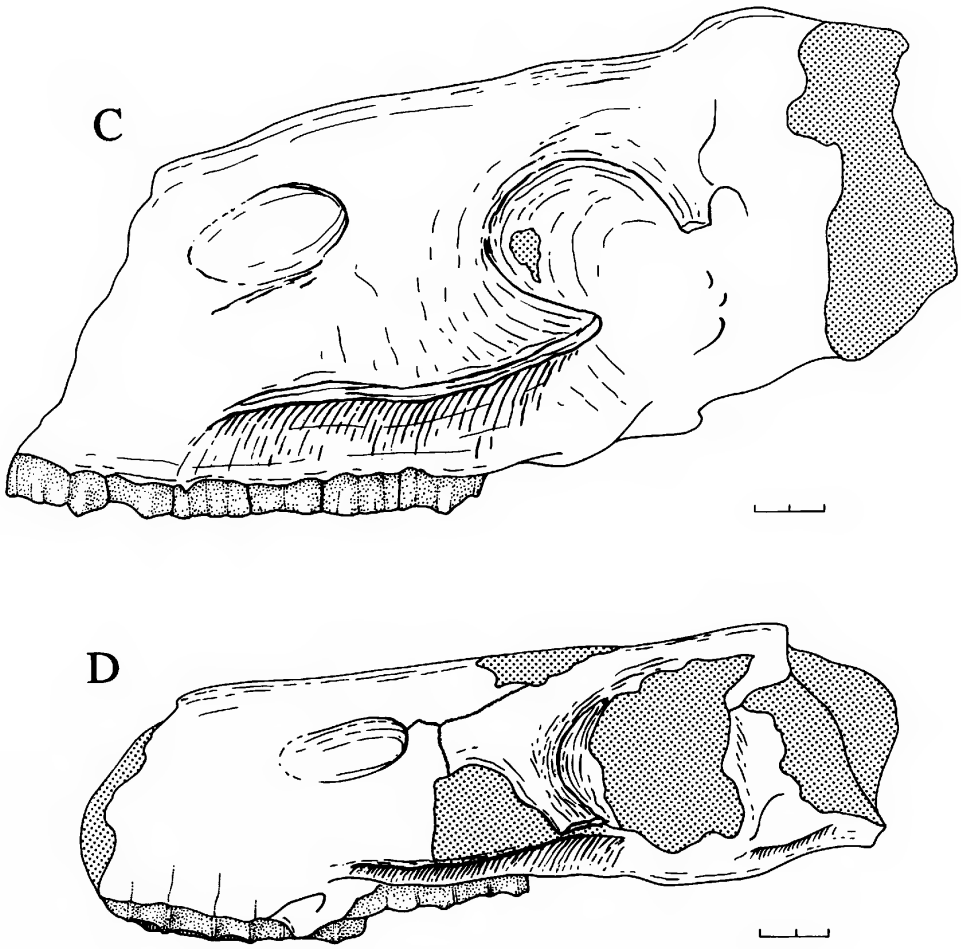

Fig. 12.—*Continued*

teeth but missing all incisors except right I1. It is a relatively large species of hipparionine, remarkable for its highly retracted nasals (nasal notch incised to P4) and elongate, slender, narrow snout. The preorbital bar is moderately long, and the lacrimal approached, but did not touch the posterior rim of the POF. The preorbital fossa is only slightly greater in its dorsoventral dimension than the distance from the facial maxillary crest to ventral fossa border. POF is subtriangular shaped and anteroventrally oriented, slightly pocketed posteriorly, with moderate medial depth, its anterior rim is distinct, and peripheral border outline is moderately strong. The deciduous cheek teeth are highly worn and retain only some occlusal features. While M1–2 remain in their crypts, they have been sectioned to show occlusal morphology. Pre- and postfossette morphology is not clearly preserved on any cheek tooth. The pli caballin is preserved on the left M1, and is bifid. DP4 and M1 preserve deeply incised hypoglyphs. DP3–4 have rounded protocones, whereas M1 has an elongate protocone.

Sefve originally identified three more specimens as belonging to "*Hipparion*" *dermatorhinum,* but these are difficult to establish as such: PMU M260 (fig. 14B), a juvenile palate fragment with right and left dP1–4, M1 and M2 (M2s erupting from their crypts); PMU M258/M259, a young adult right and left palate fragment with P2–M3 (just beginning to wear); PMU M261, a palate fragment with right and left P2–M1.

The difficulty in assigning these specimens to "*Hipparion*" *dermatorhinum* is the young age, and therefore poor occlusal morphology

development of the lectotype, and the lack of a snout and nasal notch on the other three specimens. PMU M260 does have a preorbital bar and fossa morphology closely similar to the lectotype. The cheek tooth series of PMU M259 and M260 are similar in size and morphology to the sectioned adult teeth on the lectotype, but all the characters in common are primitive and known to be distributed among a number of different species. With these reservations in mind, we hesitantly uphold Sefve's original referral of these specimens to "*Hipparion*" *dermatorhinum.*

Sefve (1927: 13–18, fig. 11) referred yet another specimen, PMU M3823, to "*Hipparion*" *dermatorhinum.* We do not maintain this referral because the specimen is a palate only, and as such, retains no facial morphology. This problem will be elaborated upon below in the hipparionine indet. section.

The American Museum collection includes a very well preserved young adult female skull and associated mandible of "*Hipparion*" *dermatorhinum* (AMNH 41-L310; figs. 14C, D, and E), from Locality 109. The AMNH specimen is virtually identical to the lectotype in preorbital fossa, nasal notch, and snout morphologies. Its maxillary cheek teeth have complex plications of the fossettes, elongate, lingually weakly flattened and somewhat lenticular-shaped protocones, and deep hypoglyphs. Pli caballins are elongate and single. In the mandibular dentition, incisors are curved, lack lingual grooves and i3 is not labiolingually constricted. Cheek tooth metaconids and metastylids are elongate. Ectoflexids do not separate metaconid/metastylid in the premolars, while they do so in the molars. Pli caballinids are rudimentary on p2–3, and absent on p4–m3. Protostylids are present on p4–m2, lacking on p2 and m3 (this last probably related to its earlier stage of wear). Linguaflexids are generally a shallow U-shape.

DISCUSSION: "*Hipparion*" *dermatorhinum* retains primitive features of the preorbital fossa including its subtriangular shape and anteroventral orientation. There is, however, some fossa reduction compared to more primitive species (re: Bernor et al., 1988, in press). Middle adult stage of wear cheek teeth are primitive in many of their character states, retaining complex, thickly banded plications of the pre- and postfossettes, and deeply incised hypoglyphs. They are derived in adult middle stage of wear by the possession of single, elongate pli caballins, and semilenticular shaped protocones. "*Hipparion*" *dermatorhinum* also has distinct autapomorphies of the facial region, including its very strongly retracted nasal notch and markedly lengthened, transversely narrowed premaxilla.

Bernor et al. (1988) have included this taxon in their phylogenetic analysis of so-called Group 1 horses (sensu Woodburne and Bernor, 1980; Bernor, 1985, and Bernor and Hussain, 1985) and found that the group is paraphyletic and "*H.*" *dermatorhinum* may represent a distinct, monospecific lineage, geographically restricted to East Asia.

"*Hipparion*" *forstenae* Zhegallo, 1971

Hipparion richthofeni Koken, sensu Sefve, 1927: 20, pl. II, figs. 5, 6; pl. III, figs. 7–10.
Hipparion richthofeni Sefve, sensu Gromova, 1952.
Hipparion plocodus Sefve, sensu Forsten, 1968, in part.
Hipparion forstenae Zhegallo, 1971.
Hipparion richthofeni Koken, sensu Zhegallo, 1978.
Hipparion plocodus Sefve, sensu Forsten, 1985, in part.
"*Hipparion*" *richthofeni,* Koken, sensu Bernor et al., 1987.

LECTOTYPE: PMU M3873.

LECTOTYPE LOCALITY: Locality 30, Baode County, Shanxi Province, China (Zdansky, 1923).

LOCALITIES: All specimens referred here are from Locality 30.

AGE: Late Miocene.

REFERRED SPECIMENS: PMU M269, skull; M3820, skull; M267, skull fragment; M268, skull fragment; M585, skull; M592, skull; M591, skull fragment; M586, skull fragment; M7357, skull fragment; M7362, skull fragment; M7359, palate; all from the type locality. AMNH specimens: 41 L352, old adult skull fragment; 41 L333, juvenile skull and mandible; 18 278, skull fragment; 19 L81, juvenile skull fragment.

GEOGRAPHIC RANGE: Baode, Shanxi, China.

DIAGNOSIS: Medium-size hipparion; POB short (24–33 mm in adults); lacrimal closely

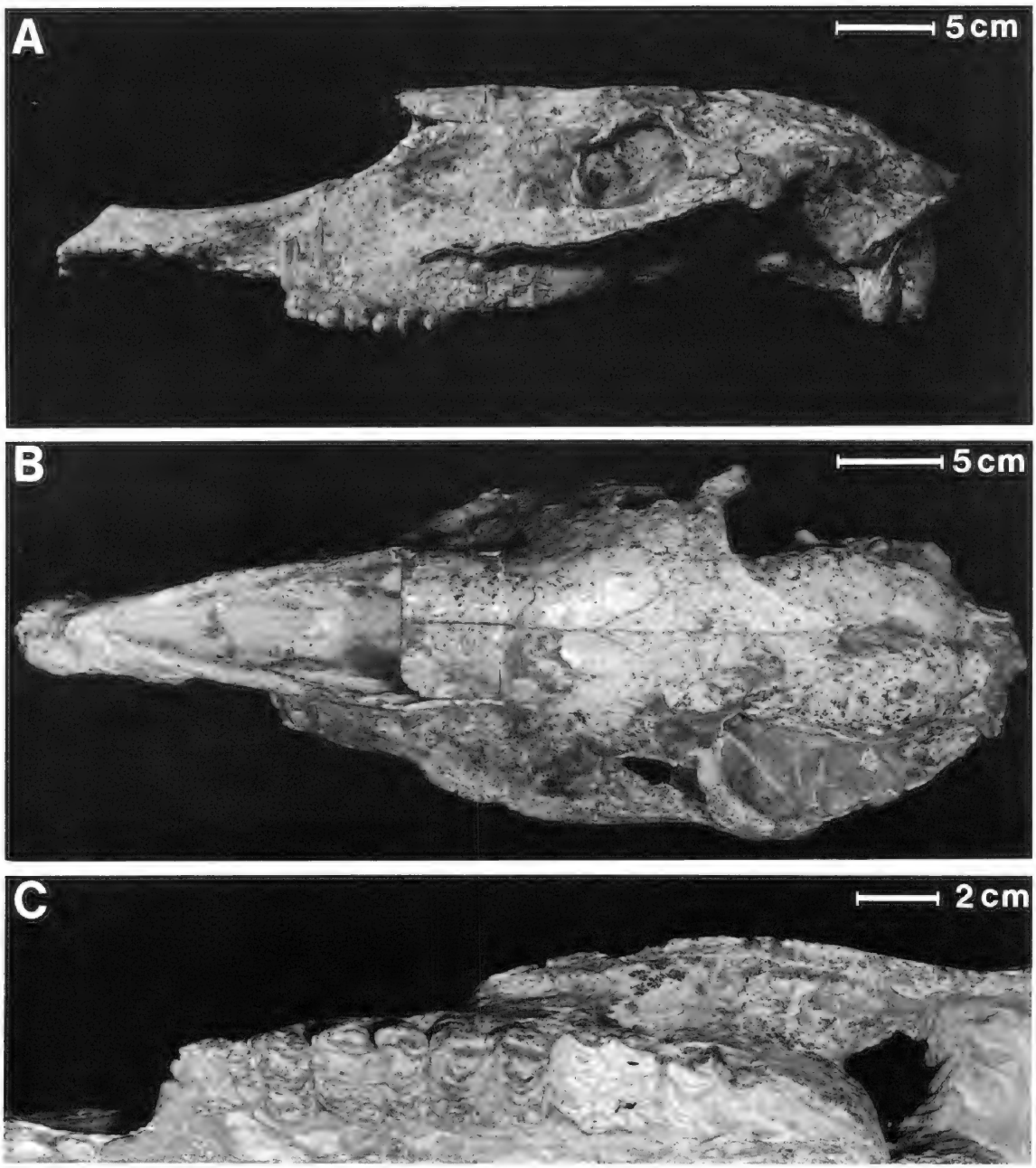

Fig. 13. "*Hipparion*" *dermatorhinum,* PMU M3872 (lectotype), from Locality 30, Baode County, Shanxi Province, late Miocene. **A.** Left lateral view of skull. **B.** Dorsal view of skull with distal nasals removed to show narial cavity. **C.** Left occlusal view of cheek teeth.

approaches or invades posterior rim of POF; POF subtriangular shaped, anteroventrally oriented, medially shallow, posterior pocketing slight, posterior rim distinctly thickened, lacking anterior rim and distinct peripheral border outline; caninus fossa distinct, but shallow; nasal bones recurved inward posteriorly at nasal notch and retracted to posterior portion of P2 or anterior portion of P3; maxillary cheek tooth row 120–146 mm long (includes young to very old adults), with moderately complex fossette plications, pli

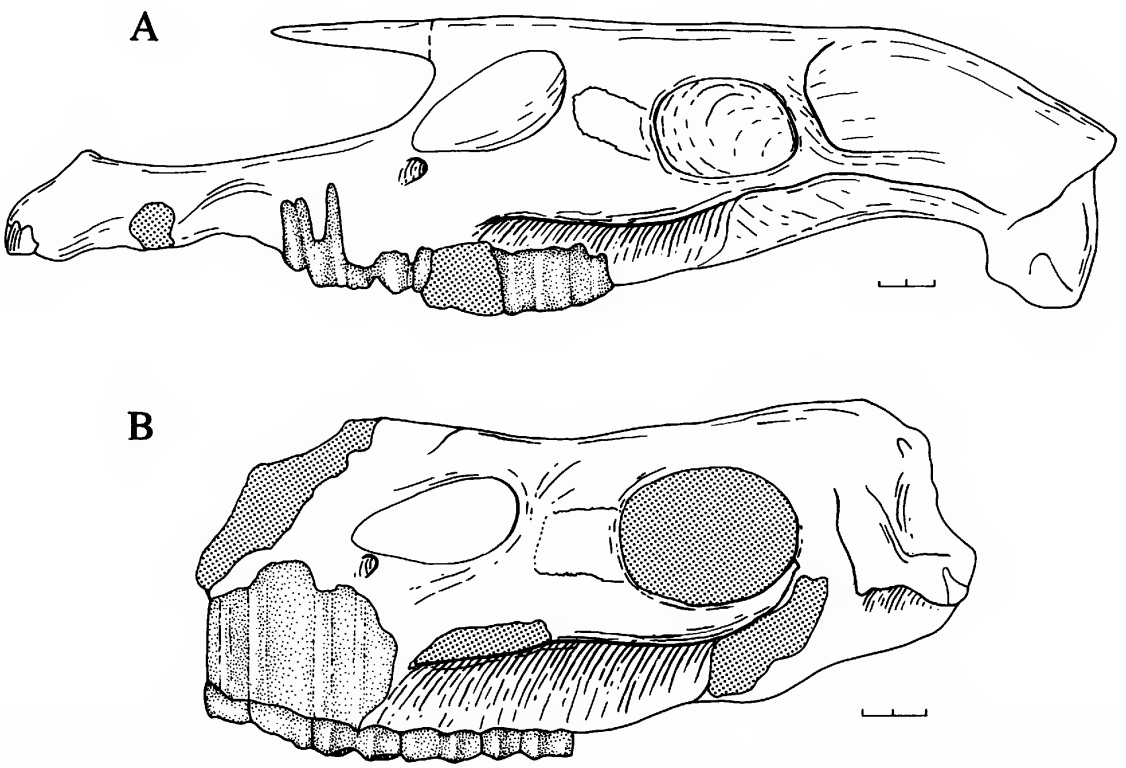

Fig. 14. Specimens referable to "*Hipparion*" *dermatorhinum,* left lateral views of skulls: **A.** PMU M3872 (lectotype, reversed; also fig. 13). **B.** PMU M260 (reversed), Locality 110; **C.** AMNH 41 L310; **D.** AMNH 41 L310, left occlusal view of maxillary cheek teeth; **E.** AMNH 41 L310, left occlusal view of mandibular cheek teeth.

caballins variably single or bifid, hypoglyphs moderately to deeply incised, protocones round to elongate.

DESCRIPTION: "*Hipparion*" *forstenae* is ostensibly the most abundant hipparion species in the PMU collection, including 12 skull specimens. PMU M3873 (lectotype; figs. 15 and 16A) is a very old adult male skull complete except for the anteriormost snout, incisors and canines; M269 (fig. 16B), an old adult male skull complete except for the cranium, posterior right orbit, anterior snout, nasals, incisors and left canine; M3820 (fig. 16C), a young adult skull fragment with all the cheek teeth, but lacking cranium, orbits and snout; M267 (fig. 16D), a subadult skull fragment with all of the cheek teeth and cranium, but lacking the posterior rims of the orbits, nasals and snout; M268 (fig. 16E), an adult skull fragment with all cheek teeth, but lacking cranium, posterior orbits, nasals and snout; M585 (fig. 16F) a complete adult male skull lacking the superior maxilla, nasals, most of left I2, left C and cranium; M592 (fig. 16G), a very old adult male skull fragment with all cheek teeth in an advanced stage of wear, lacking snout and cranium; M591 (fig. 16H), an old adult skull fragment with right P2–M2, lacking incisors, left canine and cheek tooth series, cranium and orbits; M586 (fig. 16I), an old adult skull fragment with right and left P4–M3, lacking the left orbit, cranium and snout; M7357 (fig. 16J), a very old adult skull fragment with left P2–M3, right M1–3, lacking posterior orbits, nasals, snout, and cranium; M7362 (fig. 16K), an old adult skull fragment with right M3, lacking posterior cranium and maxilla anterior to M3; M7359 (fig. 16L), an adult palate fragment with right P2–M1, left P2–M3, lacking snout, face, orbits and cranium. AMNH specimens include: 41 L352 (fig. 16O), an old adult skull fragment with I1, I3, P2–M3; 41 L333 (figs. 16P, Q, and R), a complete skull and man-

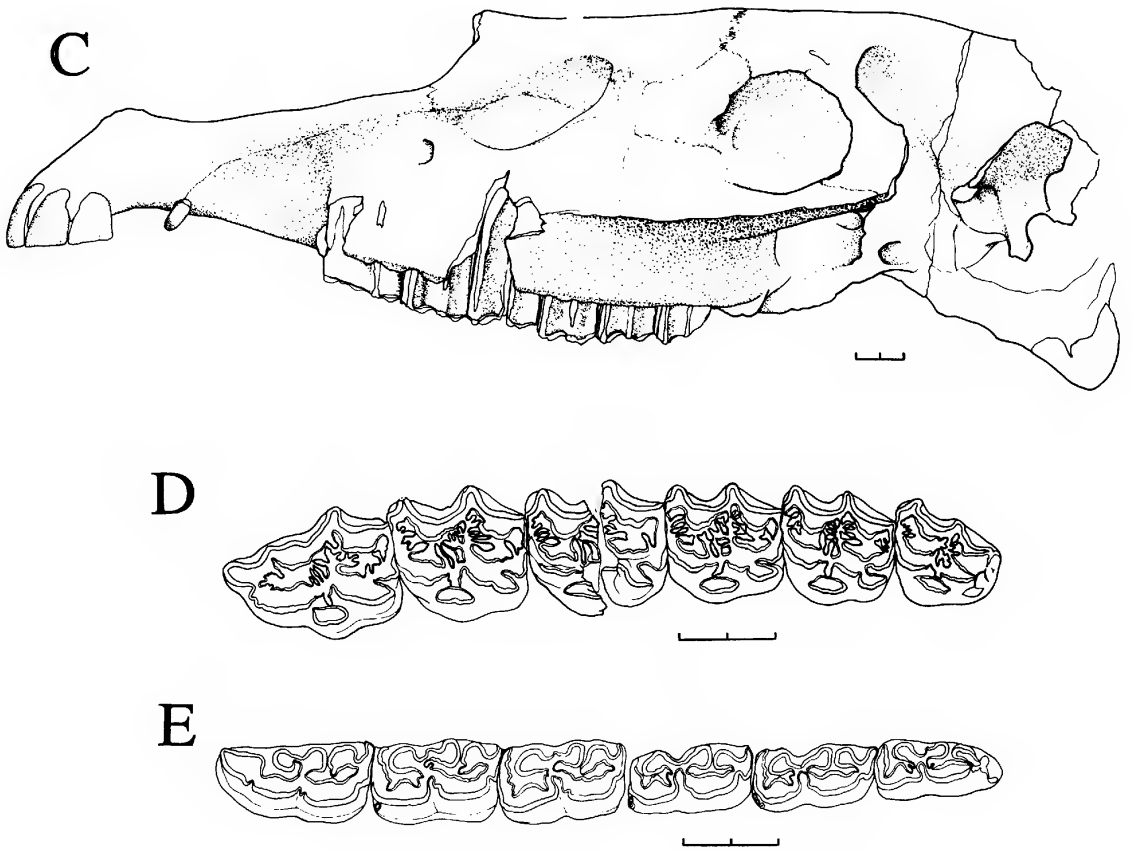

Fig. 14.—*Continued*

dible with dI1–dP4; 18 278, a juvenile skull fragment with dP1–4; 19 L81, a juvenile skull fragment with dP1–4.

The lectotype specimen of "*Hipparion*" *forstenae,* PMU M3873, has a short preorbital bar with the lacrimal invading the posterior rim of the preorbital fossa. The preorbital fossa is medially shallow; it lacks pocketing but has a prominent posterior rim, remnant depression and moderate medial depth; anterior rim and peripheral border outline are absent. The caninus fossa is present, although shallow. Likewise, the buccinator fossa is shallow. The nasal notch is retracted to a level above the interstitial surface of P2/P3 and is clearly curved inward at the nasal notch. The cheek teeth are worn far beyond their middle adult stage of wear and do not preserve details of the pre- and postfossettes and pli caballins. Likewise, the hypoglyphs on P3–4 are shallow, while on M2–3 they are moderately deeply incised. The protocones are rounded on P3–4 and M2–3, due to their advanced stage of wear. P2 has an elongate anterostyle.

PMU M269 is virtually identical to the lectotype in preorbital bar and fossa morphology. It differs, however, in having a more distinct, thickened posterior fossa rim and slightly greater medial depth. Likewise, the caninus fossa is somewhat deeper medially. The buccinator fossa is as in the lectotype. The cheek teeth are in a very advanced stage of wear and do not preserve any occlusal details. P2 has an elongate anterostyle.

PMU M3820 has character states of the preorbital fossa virtually identical to the lectotype specimen; only its medial depth is somewhat shallower. The cheek teeth are well preserved. The pre- and postfossettes are moderately complex and have bifid pli caballins (except for M3 where they are single),

Fig. 15. "*Hipparion*" *forstenae,* PMU M3873 (lectotype), from Locality 30, Baode County, Shanxi Province, late Miocene. **A.** Right lateral view of skull. **B.** Right occlusal view of cheek teeth.

probably due to its early stage of wear. The hypoglyphs are deeply incised on all cheek teeth. The protocones have an elongate to rounded morphology, except for M3 which is elongate and lingually flattened due to its very early stage of wear.

PMU M267 shares all the character states of the preorbital bar and preorbital fossa that the lectotype has, except the fossa's shallower medial depth. The cheek teeth have moderately complex pre- and postfossette morphology, or weakly bifid pli caballins, and deeply incised hypoglyphs. The protocones are lingually flattened on P2–3, due to their early stage of wear, and elongate to rounded on the remaining cheek teeth. The P2 anterostyle is elongate. A middle stage of wear adult would probably have had a cheek tooth occlusal morphology as in the lectotype.

PMU M268 shares all the preorbital fossa characteristics of the lectotype specimen, except that its medial depth is somewhat greater. The caninus and buccinator fossae and nasal notch are not preserved. The cheek tooth pre- and postfossettes are moderately complex on all the cheek teeth. The pli caballins are bifid on P3–M1, but single on P2 and M2–3. The hypoglyphs are deeply incised on all cheek teeth. The protocones are rounded on all cheek teeth.

PMU M585 is virtually identical to the lectotype in its preserved facial morphology, except for the preorbital fossa posterior rim which is more prominent. Details of the preorbital fossa medial wall, anterior rim, and peripheral border outline are not preserved. The cheek teeth all have moderately complex plications of the pre- and postfossettes. Pli

caballins are single on all cheek teeth except M1, on which it is bifid. The hypoglyphs are deeply incised on the premolars and slightly less incised on M1–2. The protocones show some lingual flattening due to their early wear, especially on the premolars; but become less flattened and more oval-shaped in the later wear stages present on M1–2.

PMU M592 is identical in facial morphology to the lectotype, except that it does not preserve the caninus and buccinator fossae, nor the nasal notch. The cheek teeth are in such an advanced stage of wear that they do not preserve any occlusal details.

PMU M591 shows some slight differences from the lectotype in facial morphology. The preorbital fossa has a more distinct posterior rim, its medial depth is slightly greater, and the anterior rim is slightly expressed instead of being absent. The cheek teeth are very worn, but preserve some morphological details. The pli caballins are faintly bifid on P3–M1, but single on M2. The hypoglyphs are moderately incised on P3, and more shallowly incised on P4 and M1–2. The protocones are rounded on P3–M2. The departure of this specimen from others of the hypodigm in cheek tooth morphology is probably due to its advanced stage of wear.

PMU M586 also shows slight differences from the lectotype in facial morphology. The preorbital fossa has a slightly deeper medial depression. The caninus fossa is as in the lectotype, while the buccinator fossa is not preserved. The cheek teeth are too worn to preserve any meaningful occlusal morphology.

The last three PMU specimens, M7357, M7362, and M7359 are the most fragmentary ones of the hypodigm. The first two do not differ in any essential details of facial morphology from the lectotype. These two specimens' cheek teeth are too worn to reveal any occlusal details. PMU M7359 has only the inferior portion of the face preserved, but reveals morphology of preorbital fossa medial depth, anterior rim, peripheral border outline and ventral border contour identical to that seen in the lectotype. Likewise, there is a shallow caninus fossa. The cheek teeth are also morphologically identical with the rest of the hypodigm. The pre- and postfossettes are complex on P3 and moderately complex on P4–M3. The pli caballins are single on all cheek teeth. The hypoglyphs are moderately deeply incised on P3 and M1, deeply incised on P4 and M2–3. The protocones are lingually flattened on P3–4 and M2, rounded on M1 and elongate on M3.

There are two PMU specimens which we refrain from referring to "*Hipparion*" *forstenae* but are morphologically closest to this taxon and are important to describe here: PMU M588 (fig. 16M) and PMU M3821 a + b (fig. 16N). PMU M588 (Locality 31) is similar to "*H.*" *forstenae,* but lacks some important characteristic features. The preorbital bar is relatively short, and within the range of variation for "*Hipparion*" *forstenae.* The lacrimal is distinct in outline, and closely approaches the posterior rim of the preorbital fossa but does not touch it. The nasal notch appears to be retracted to mesostyle of dP2, which is somewhat less than in other individuals that preserve this structure. The M1 is not yet worn enough to reveal middle adult stage of wear morphology. However, the deciduous premolars show a moderate plication amplitude, simplification of the pli caballins, and oval to rounded protocones. If this specimen is indeed referable to "*Hipparion*" *forstenae,* which seems plausible, then it would be the only individual yet known from the PMU collection to be found at a locality other than Locality 30.

One further PMU specimen shows some affinities with the hypodigm of "*Hipparion*" *forstenae,* PMU M3821 A + B (fig. 16N, Locality 30). This specimen has been enigmatic since its referral by Sefve (1927: pl. IV, figs. 14, 15) to *Hipparion fossatum* (= "*H.*" *coelophyes* here). It is a virtually complete skull with an associated mandible of a very old individual, which has been dorsoventrally sectioned through the preorbital bar along an oblique coronal plane. It lacks the nasals and the dorsal portion of the preorbital fossa, and the cheek teeth are in too advanced a stage of wear to be taxonomically useful. The preorbital bar is distinctly shorter than "*Hipparion*" *coelophyes,* PMU M3690, and the remainder of the "*Hipparion*" *coelophyes* hypodigm. Rather, the length of the preorbital bar is within the range of variation of "*Hipparion*" *forstenae.* However, we do not find it advisable to refer this specimen to any tax-

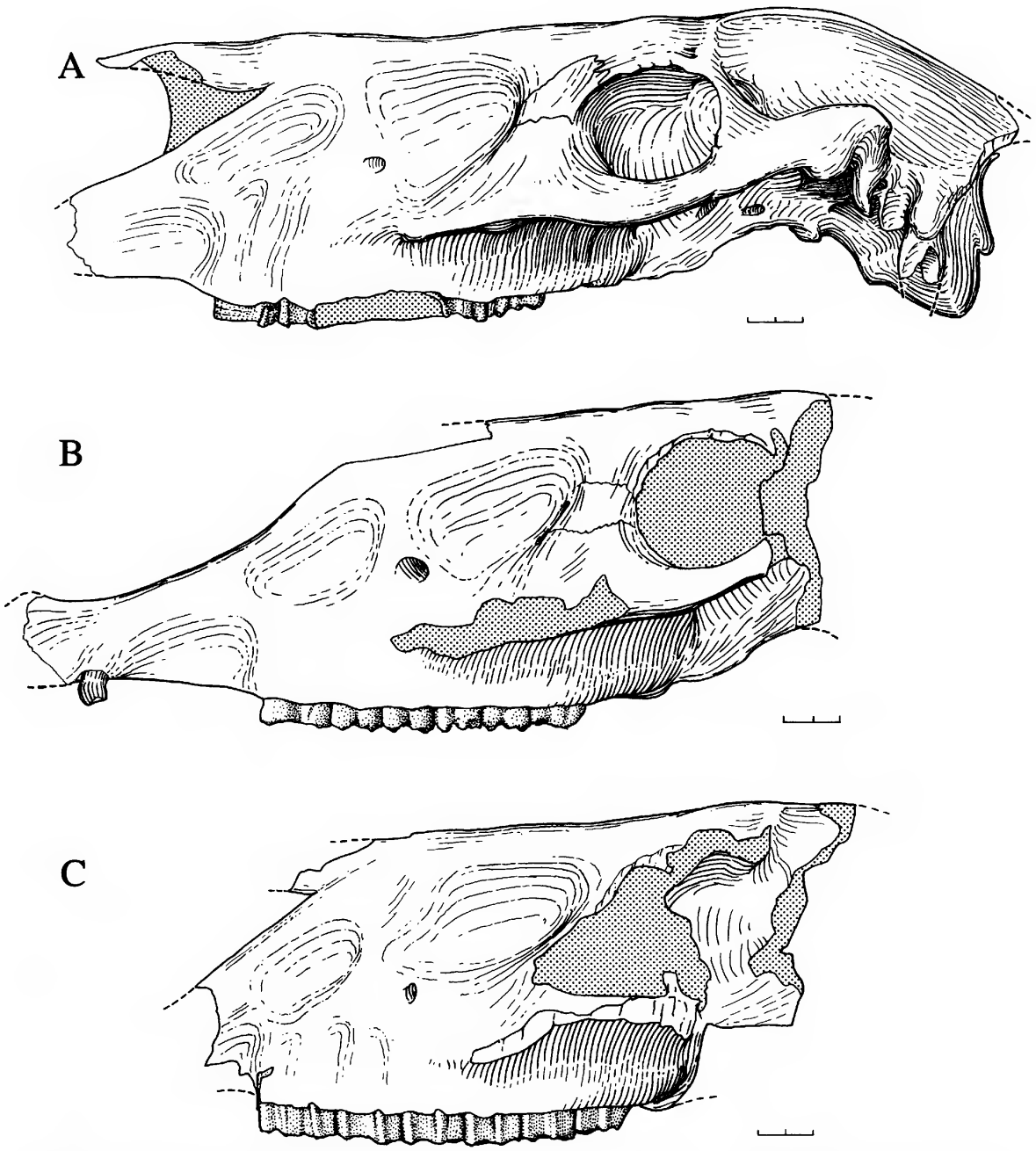

Fig. 16. Specimens referable or potentially referable to "*Hipparion*" *forstenae,* left lateral views (except Q and R), all Locality 30. **A.** PMU M3873 (lectotype, reversed; also fig. 15). **B.** PMU M269 (reversed). **C.** PMU M3820 (reversed). **D.** PMU M267. **E.** PMU M268 (reversed). **F.** PMU M585 (reversed). **G.** PMU M592 (reversed). **H.** PMU M591. **I.** PMU M586 (reversed). **J.** PMU M7357. **K.** PMU M7362 (reversed). **L.** PMU M7359 (reversed). **M.** PMU M588 (reversed). **N.** PMU M3821 A + B. **O.** AMNH 41 L352. **P.** AMNH 41 L333. **Q.** AMNH 41 L333 (occlusal view, right maxillary dentition). **R.** AMNH 41 L333 (occlusal view, right mandibular dentition).

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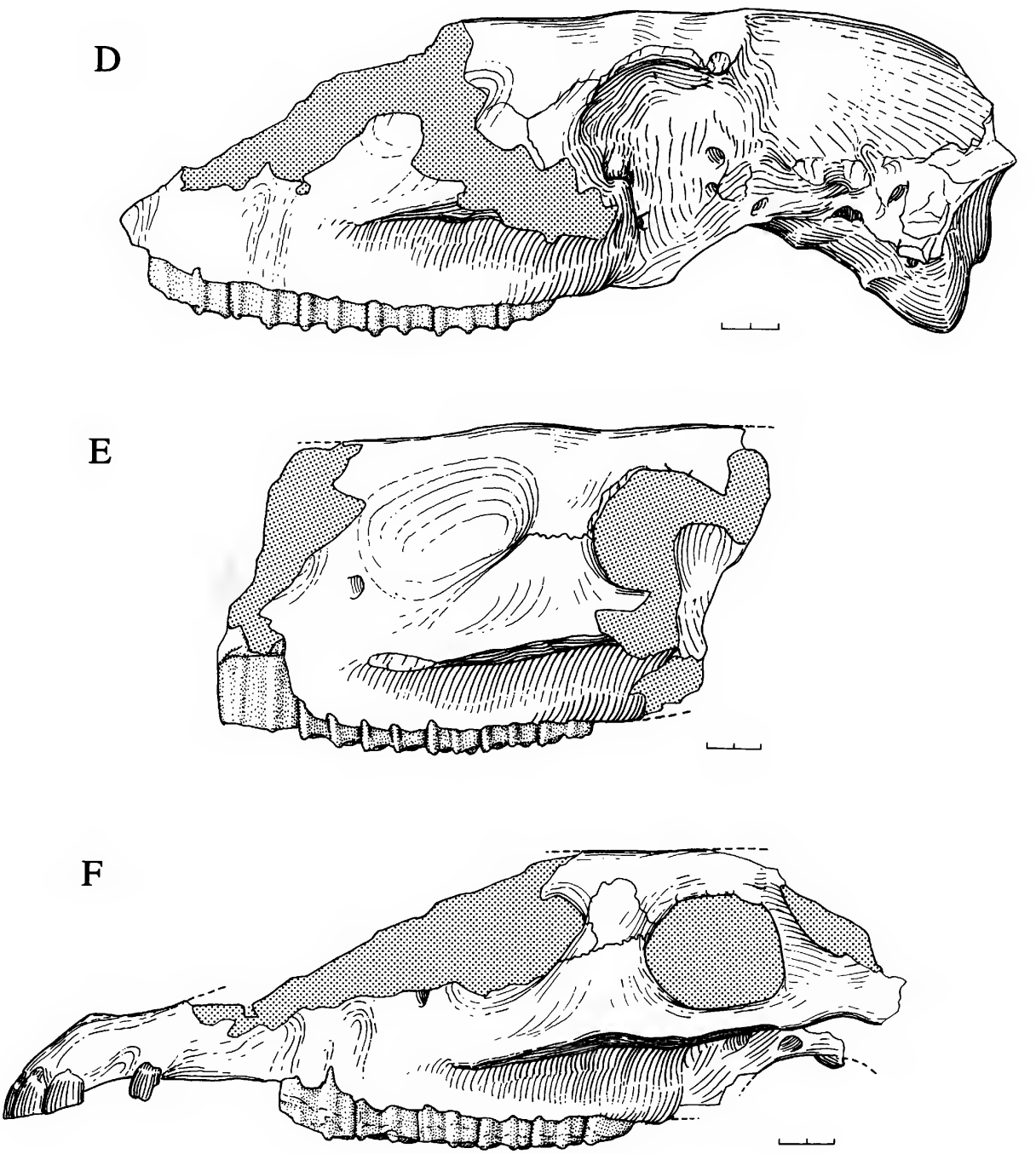

Fig. 16.—*Continued*

on, let alone make it the lectotype of "*Hipparion*" *coelophyes* as done by Forsten (1985: 123).

Of the four AMNH specimens that we refer to "*Hipparion*" *forstenae,* only one, 41 L352, is an old adult. 41 L352 shares all the characters of the facial region that the lectotype exhibits: preorbital fossa closely approached by the lacrimal, weakly defined peripherally, shallow medially; caninus fossa is distinct,

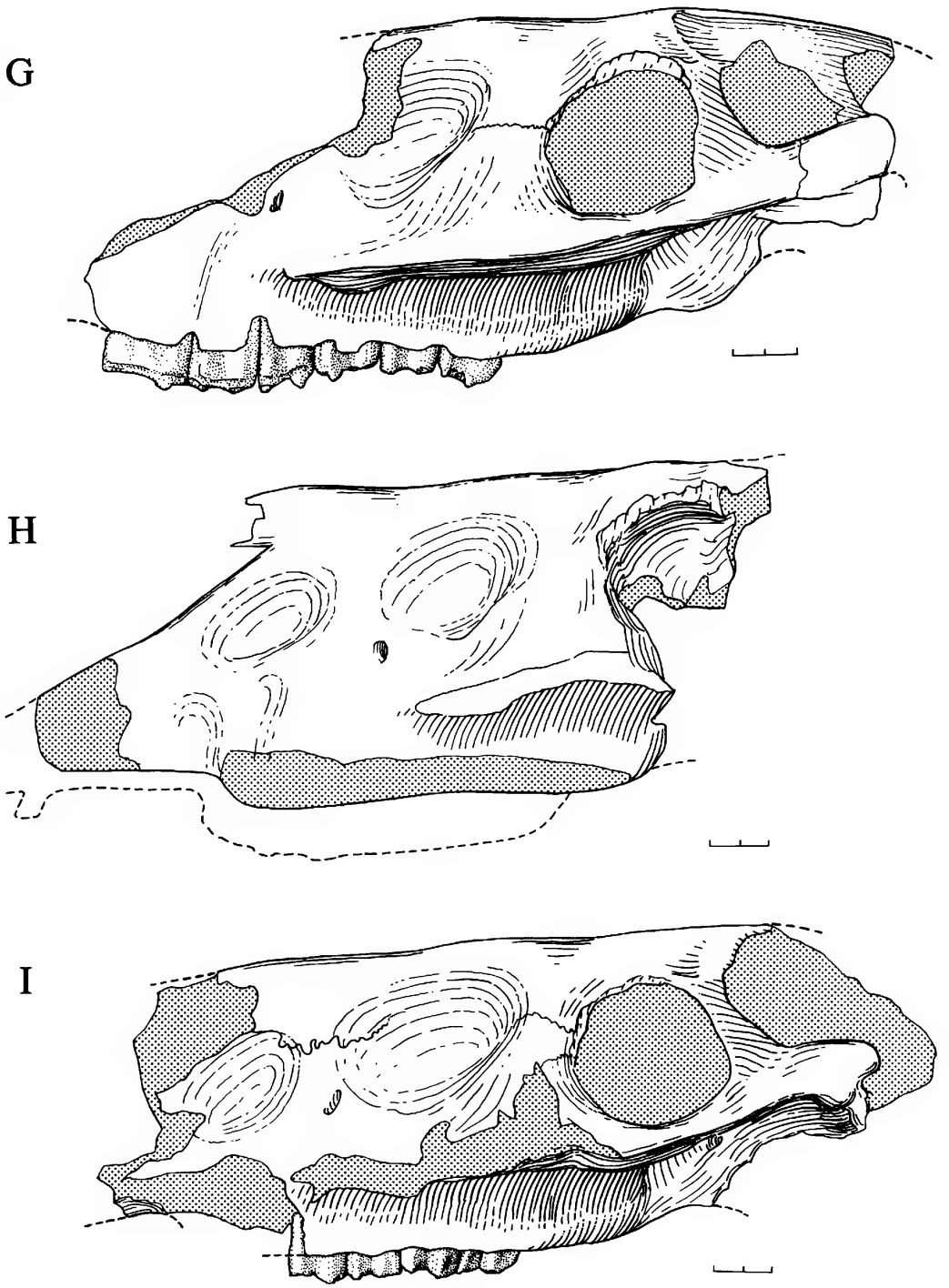

Fig. 16.—*Continued*

although shallow; nasal notch is retracted to posterior P2 (slightly further anteriorly). Because of cheek tooth advanced stage of wear, pre- and postfossettes generally show no plis, pli caballins are single, hypoglyphs are shallowly incised.

The three juvenile AMNH skulls, 18 278, 19 L81, and 41 L333 show a remarkably sta-

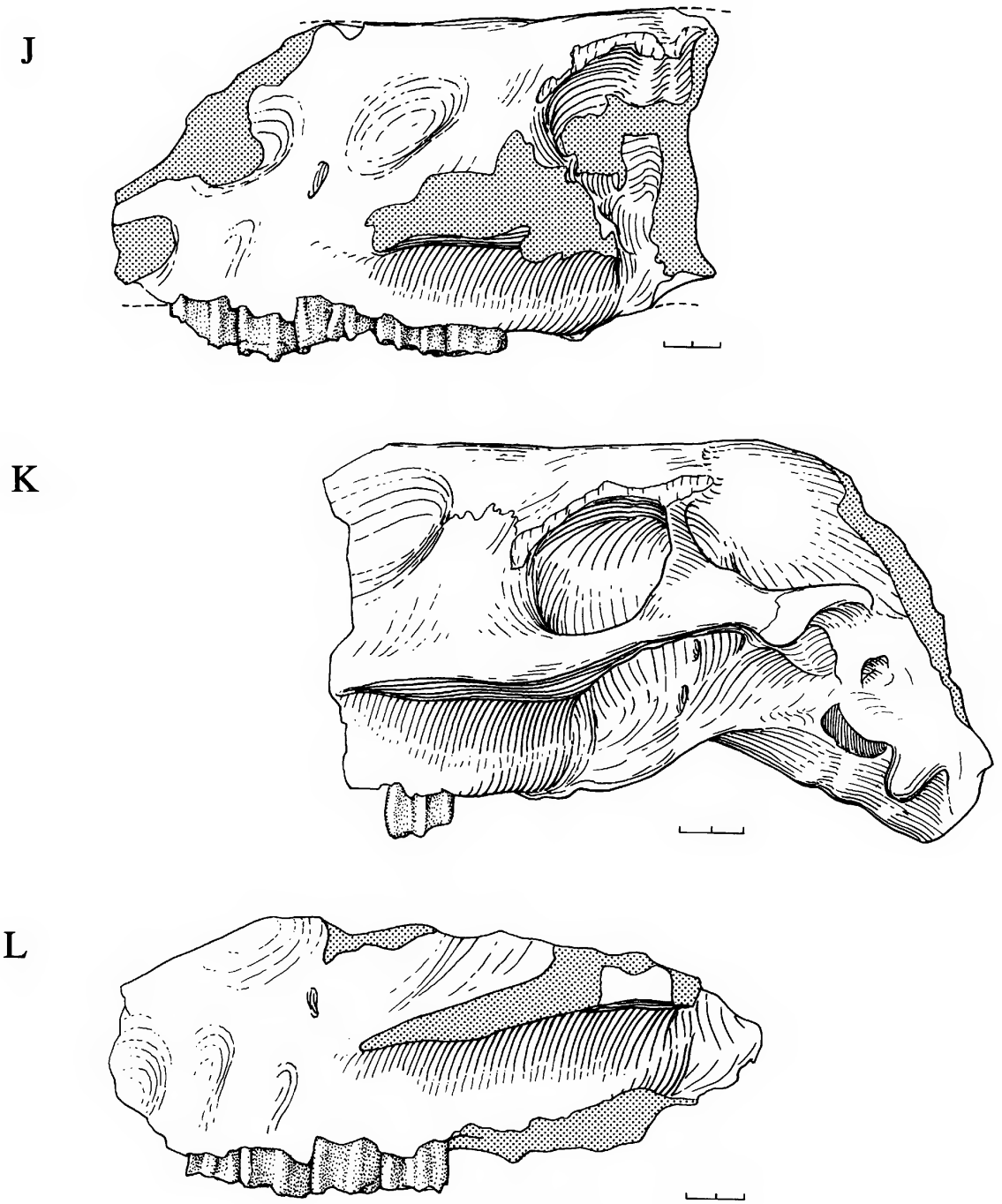

Fig. 16.—*Continued*

bility of facial characters in their virtual morphological identity to the remainder of our hypodigm. 41 L333 is by far the best preserved specimen of the juvenile individuals, and includes a complete skull and mandible (in block). 41 L333 clearly exhibits the salient facial characters of the species including: a distinct anteroventral orientation of the POF (more distinct than seen in the adult members of the species); lacrimal does not touch the POF, unlike in the adult condition; nasals all retracted above mesostyle of dP2 (slightly

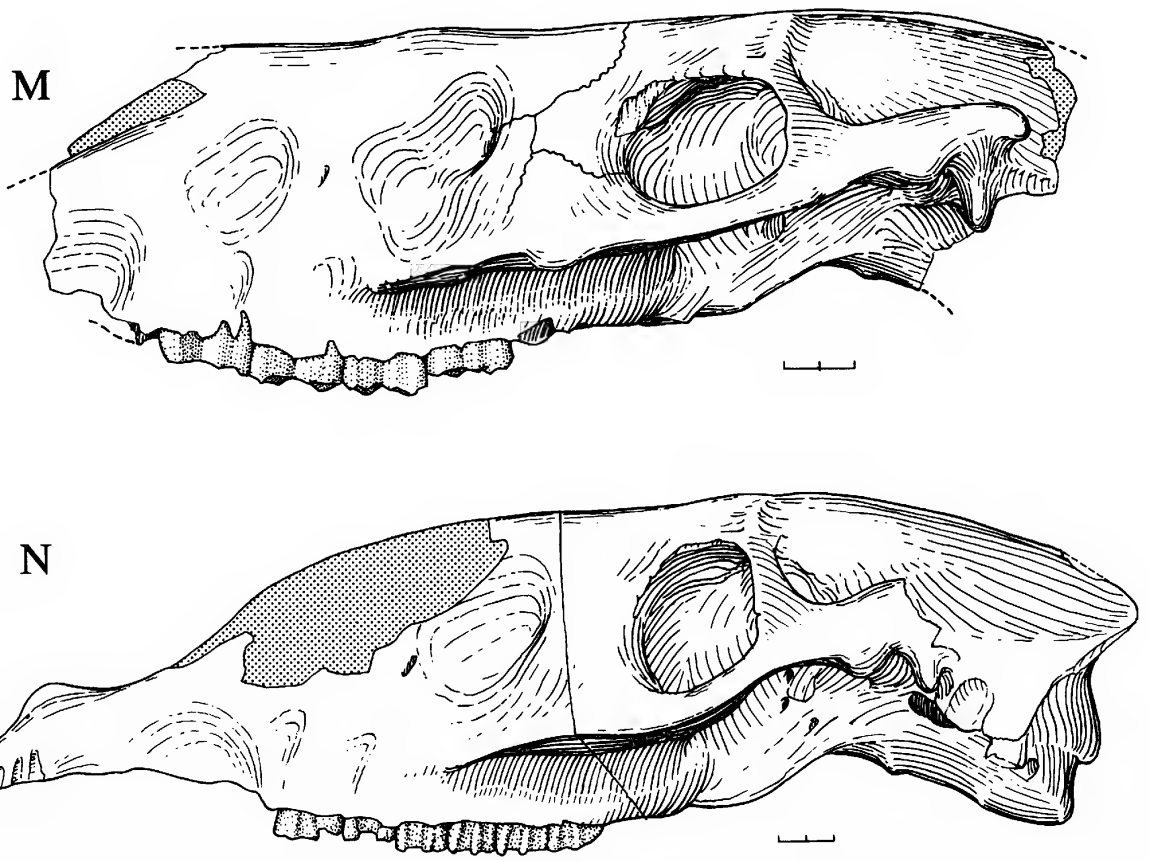

Fig. 16.—*Continued*

more anterior than in adult individuals), and are curved distinctly inward.

DISCUSSION: "*Hipparion*" *forstenae* has the most complex nomenclatural history of all Chinese hipparionines. Koken (1885) erected the taxon "*H.*" *richthofeni* based on 11 isolated cheek teeth of unknown provenance (Chinese drugstores). Schlosser (1924) followed by referring another assemblage of 850 isolated teeth from Harr Obo to "*H.*" *richthofeni.* Sefve (1927) injudiciously referred specimens in the Uppsala collection to *H. richthofeni* with virtually no justification. Gromova (1952) correctly argued that none of Koken's (1885) referred sample was diagnostic enough to warrant species recognition, while Sefve's (1927) material represented, without a doubt, a valid and distinct species. However, Gromova (1952) failed to provide a new name for this taxon. Forsten (1968) rejected Gromova's (1952) conclusions about the Uppsala "*H.*" *richthofeni* assemblage, synonymizing it with a highly variable taxon, *H. plocodus.* Zhegallo (1971) revived Koken's taxon "*H.*" *richthofeni,* choosing a broken P3 (Koken, 1885, pl. IV, fig. 5) as lectotype of the species. Zhegallo (1971) claimed that this tooth was housed in the British Museum (Natural History) (BMNH M28584), but this was later denied by Forsten (1978). However, Zhegallo (1971) directly addressed the nomenclatural problem surrounding the Uppsala collection of "*H. richthofeni*" by erecting the taxon *H. forstenae,* based on the first specimen figured by Sefve (1927: pl. II, figs. 5 and 6). Unfortunately, Zhegallo (1978) later abandoned the use of this nomen altogether. We agree with Gromova (1952) and Forsten (1968) that the taxon "*H.*" *richthofeni* as defined by Koken (1885) and Schlosser (1924) has limited value and should be abandoned. Moreover, we follow Zhegallo's (1971) original recommendation that the Uppsala assemblage, formally

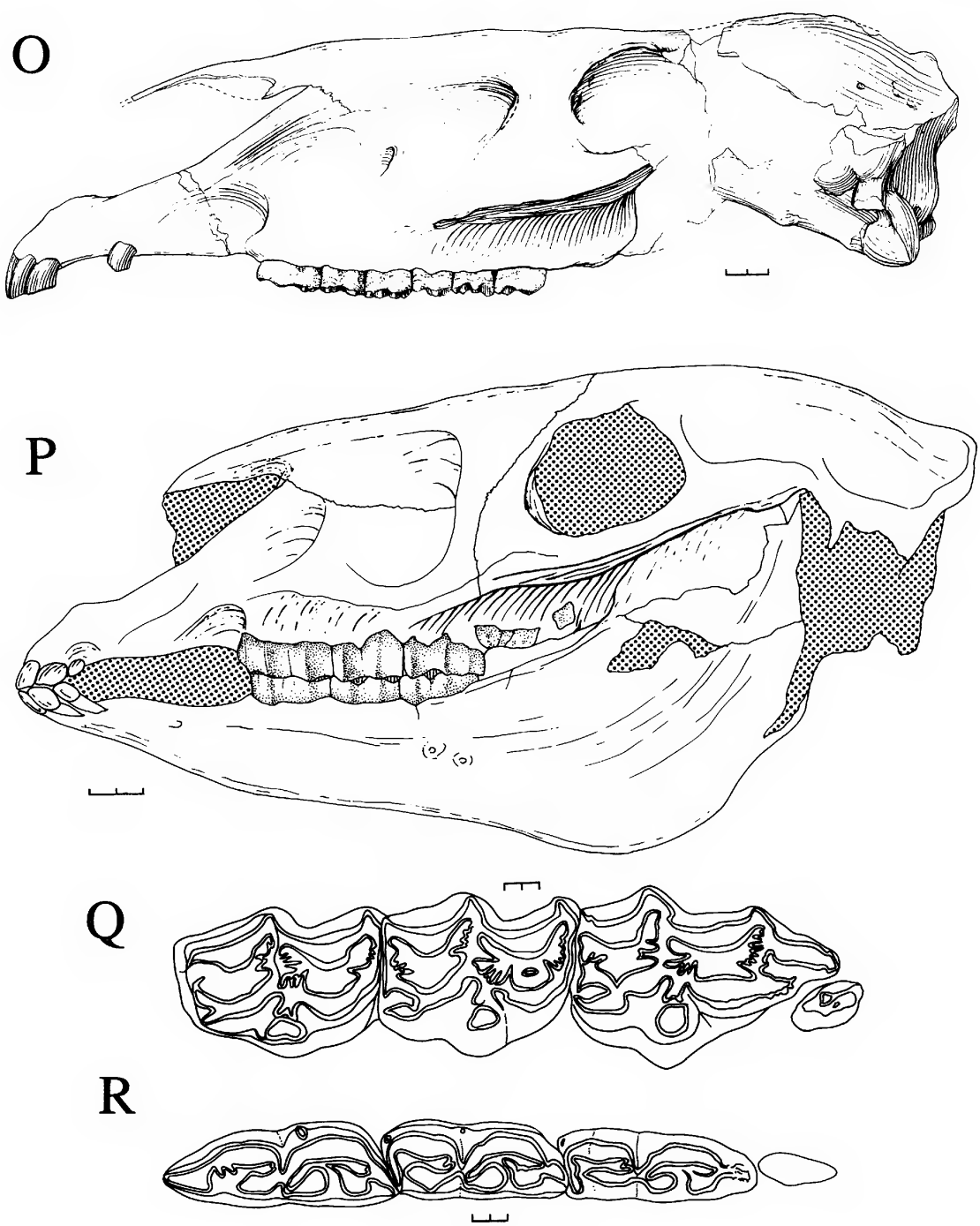

Fig. 16.—*Continued*

referred to *Hipparion richthofeni* by Sefve (1927), should henceforth be known as "*Hipparion*" *forstenae.*

The PMU assemblage of "*Hipparion*" *forstenae* is remarkably homogeneous in its facial and maxillary cheek tooth morphology. In features of the preorbital fossa complex (including the short preorbital bar with the lacrimal touching or invading the posterior rim, preorbital fossa with a faint subtriangular shape and anteroventral orientation, and presence of both buccinator and caninus fos-

sae), "*H.*" *forstenae* is clearly a member of an Old World hipparion lineage distinct from *Hipparion* s.s. (sensu Woodburne and Bernor, 1980; Bernor and Hussain, 1985; Bernor, 1985; Bernor et al., 1987; Bernor et al., in press; Woodburne, 1989). Qiu et al. (1987) recognized "*H.*" *forstenae*'s affinities with some European species (citing the Samos species "*H.*" *proboscideum*) and the Pliocene Chinese horse "*H.*" *licenti,* and referred them to a new subgenus *Hipparion* (*Cremohipparion*). Bernor et al. (in press) have followed, stating that *Hipparion* (*Cremohipparion*) (Qiu et al., 1987) conforms to Woodburne and Bernor's (1980) Group 2, and is quite distinct from *Hipparion* s.s., and raised it to the genus rank of *Cremohipparion* recognizing a total of six species: *Cremohipparion mediterraneum* (the genotype species), *C. moldavicum, C. matthewi, C. proboscideum, C. forstenae,* and *C. licenti.*

Proboscidipparion sinense
Sefve, 1927

Proboscidipparion sinense Sefve, 1927: 55, pl. VI, figs. 22–24, pl. VII, figs. 25 and 26.

HOLOTYPE: PMU M3925.

TYPE LOCALITY: Locality 39, Langou Mianchi County, Henan Province, China (Zdansky, 1923).

AGE: Late Pliocene and early Pleistocene.

GEOGRAPHIC RANGE: Mianchi County, Henan Province; Nihewan County, Hebei Province; Yushe County, Shanxi Province, China.

DIAGNOSIS: Very large hipparion; lacking POF; nasals hyper-retracted to posterior half of M3; snout elongate; maxillary and mandibular incisors with longitudinal grooves; canines lacking; maxillary cheek tooth row 165+ mm, with very complex fossette plications; pli caballins bifid to complex, hypoglyphs deeply incised, protocones triangular-shaped being anteroposteriorly long and lingually flattened; mandibular cheek teeth with deeply incised broadly U-shaped linguaflexids, metaconids and metastylids with angular opposing borders, bifid m3 hypoconulids.

DESCRIPTION: There is a single, old adult skull of *Proboscidipparion sinense,* the holotype (fig. 17A–D), in the PMU collections. The skull is complete, has an accompanying lower jaw (fig. 18A, B), and is remarkable in its very large size, long snout, lack of a preorbital fossa, and retraction of the nasals nearly to the anterior border of the orbits. Functionally associated with this is a broadly expanded, medially deep buccinator fossa. The incisors are large, I3 is very long mesiodistally; all incisors have distinct grooves on their labial and lingual surfaces; occlusal dentine lakes are small and round in I1 and I3, more mesiodistally elongate and irregular in I2. There are no canines or canine alveoli. The cheek teeth are in a very advanced stage of wear. However, P3–4 and M2–3 are well enough preserved to reveal that this specimen had extremely complex plications of the pre- and postfossettes, complex pli caballins, deeply incised hypoglyphs and triangular-shaped, elongate protocones with a flattened lingual aspect. The P2 anterostyle is elongate.

The associated mandible is virtually complete, lacking only the right ascending ramus, the crowns of right i2–3 and left p3. The incisors are curved, have labial and lingual grooves as in their maxillary homologs and the infundibula are all small, centrally placed, and circular. There are neither canines nor canine alveoli. The p2 paraconid is elongate. In the premolars, the ectoflexids are shallow and do not separate metaconid/metastylid; there are neither pli caballinids nor protostylids; linguaflexids are shallow on p2, deep and broadly U-shaped on p3–4; p2 metaconid is rounded while p3–4 are angular; all metastylids have strongly angled anterior borders; entoflexids and metaflexids are elongate and have simple enamel borders. The molars have deeply incised ectoflexids separating metaconids and metastylids; there are no pli caballinids; there is a very small protostylid on m1 and none on m2–3; metaconids and metastylids have sharply angular opposing surfaces separated by deeply incised, broadly U-shaped linguaflexids; entoflexids and metaflexids are as in the premolars.

DISCUSSION: *Proboscidipparion sinense* is a Nihowan age (= Plio-Pleistocene) hipparionine restricted to North China. Sefve (1927) originally erected *Proboscidipparion* as a genus because of its very large size and presumed possession of a proboscis (strongly retracted nasals). Teilhard de Chardin and

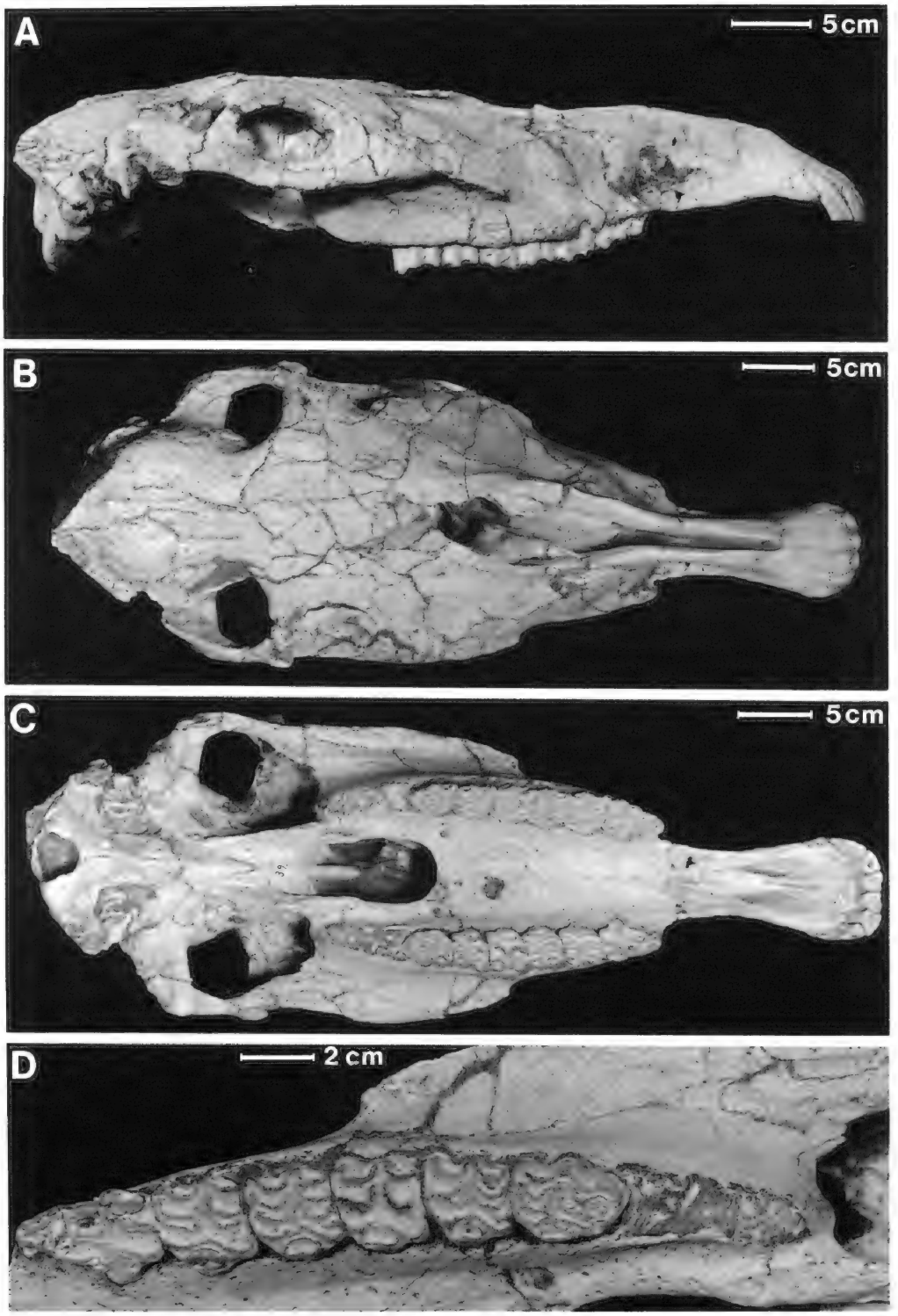

Fig. 17. *Proboscidipparion sinense,* PMU M3925 (holotype), from Locality 39, Langou, Mianchi County, Henan Province, late Pliocene or early Pleistocene. **A.** Right lateral view of skull. **B.** Dorsal view of skull. **C.** Ventral view of skull. **D.** Left occlusal view of cheek teeth.

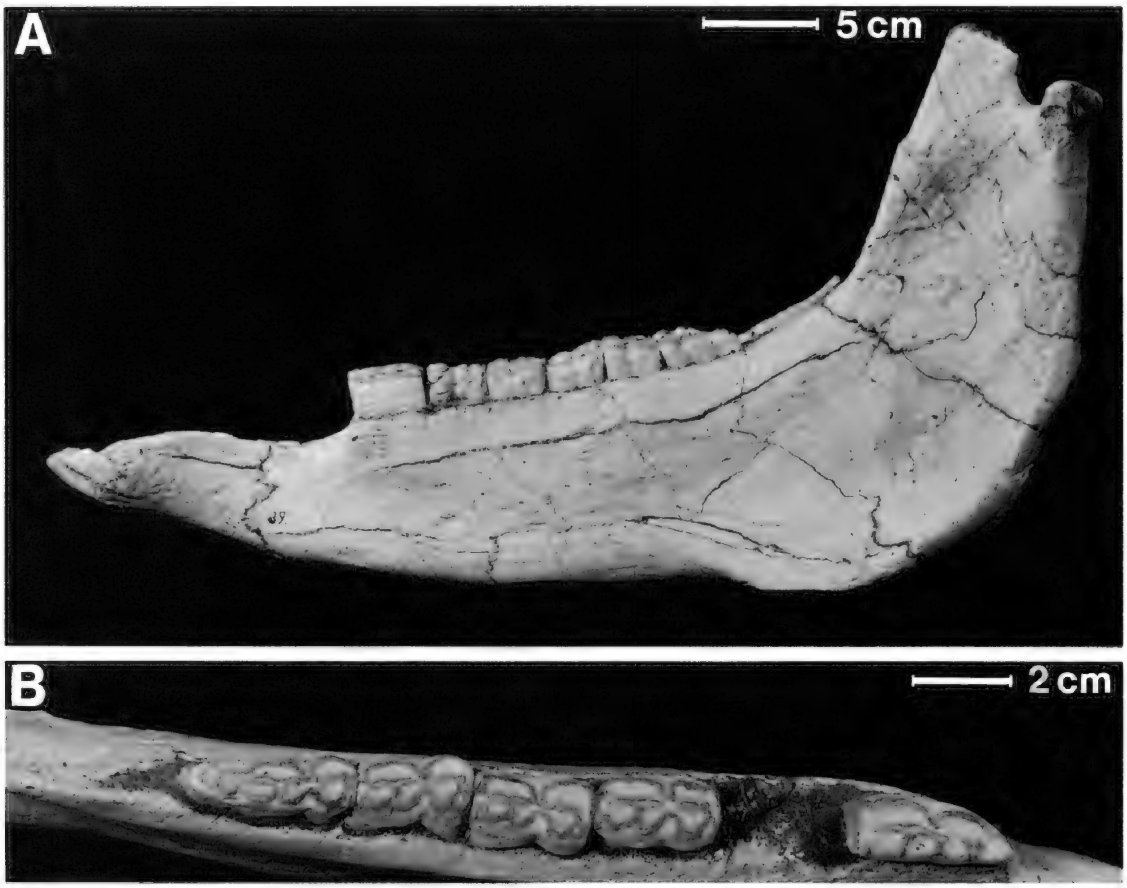

Fig. 18. *Proboscidipparion sinense,* PMU M3925 (holotype), from Locality 39, Langou, Mianchi County, Henan Province, late Pliocene or early Pleistocene. **A.** Left lateral view of mandible. **B.** Left occlusal view of cheek teeth.

Piveteau (1930) rejected a genus-level distinction and, instead, proposed a subgeneric one. Gromova (1952) recognized the generic distinction of *Proboscidipparion sinense,* citing "unique" *Equus*-like morphologic features including: large size, absence of a facial fossa, elongate protocone, caballoid "double-knot" (= metaconid/metastylid) of the lower cheek teeth, shape of the distal sagittal keel of metapodial IIIs, and weakly developed lateral digits. She believed that *Proboscidipparion sinense* shared unique evolutionary characters with "*Hipparion*" *houfenense* including metaconid/metastylid morphology and massiveness of metapodials and phalanges. She further remarked that other Chinese hipparionines, namely "*Hipparion*" *dermatorhinum,* showed some nasal retraction, and implied a potential phylogenetic relationship to that species. Forsten's (1968, 1984, 1985) opinion has closely coincided with Gromova's.

Qiu et al. (1987) have recently reviewed this taxon and supported Teilhard de Chardin and Piveteau's proposal that *Proboscidipparion* be recognized as a subgenus of *Hipparion.* They have proposed this position because of a recent collection of new fossil material from the Yushe Basin which comes from older, Pliocene age horizons, and which they believe to represent a species ancestral to *P. sinense.* This species, "*Hipparion*" (*Proboscidipparion*) *pater,* is approximately 85 percent the size of *P. sinense*; it has a shorter distance between M3 and the orbit, the sagittal crest is longer, the incisive foramen is

not reduced in size and, as in *P. sinense,* it lacks a preorbital fossa, and the nasals are strongly retracted. Qiu et al. (1987) further reported that the mandibular cheek teeth are identical to those of Matsumoto's taxon "*H.*" *richthofeni* mut. *pater,* and hence they utilized the available subspecies name for his species. In so doing, Qiu et al. (1987) identified the following mandibular cheek tooth characters diagnostic of this species: metaconid/metastylid is "houfenoid" (= caballoid of Gromova, 1952 and Forsten, 1968, 1984, 1985), with very wide linguaflexid; hypoflexid is long, narrow and weakly developed, without bending lingually at its anterior end; cheek teeth are remarkably high crowned (57 mm) and narrow (13.5 mm), with well-developed protostylid, strongly curved posteriorly; pli caballinid and anteplicaballinid are not clearly developed.

Flynn and Bernor (1987) recently described an early Pliocene vertebrate fauna from Kholobolochi Nor, Mongolia, which included a hipparionine mandible and isolated cheek tooth material which they assigned to "*Hipparion*" *houfenense.* This material is smaller than the younger Nihowan age "*Hipparion*" aff. *houfenense* (AMNH F:AM 11182; MacFadden, 1984: 188, fig. 151), and is virtually identical in size and morphology to the similarly aged species "*Hipparion*" (*P.*) *pater* (Qiu et al., 1987). Flynn and Bernor (1987) further identified a number of skull and cheek tooth characters as synapomorphies between *Proboscidipparion sinense* and "*Hipparion*" *houfenense,* including: (1) absence of preorbital fossa; (2) maxillary and mandibular incisors with deeply incised longitudinal grooves; (3) I3s with labiolingual constriction of the most distal portion; maxillary cheek teeth with—(4) subtriangular-shaped elongate protocones with a flattened lingual aspect; (5) elongate, bifid pli caballins; (6) complex plications of the fossettes; (7) deeply incised hypoglyphs; mandibular cheek teeth with—(8) deeply incised, broad U-shaped linguaflexids, (9) metaconid and metastylid with strongly angular opposing surfaces, (10) m3 with distinctly bilobed hypoconulids. *Proboscidipparion sinense* and "*Hipparion*" aff. *houfenense* (F:AM 111820) both are larger sized than "*H.*" *houfenense* (see Flynn and Bernor, 1987: 8, 9, tables 1, 2).

Proboscidipparion sinense principally differs from "*Hipparion*" *houfenense* and F:AM 111820 in its strongly retracted nasals (to mesostyle of M3 versus parastyle of P2), but also appears to have more complex fossette and pli caballin ornamentation. Flynn and Bernor (1987) proposed that *P. sinense* and "*H.*" *houfenense* (= "*Sivalhippus*" *houfenense* of Bernor et al., in press) are phylogenetically related to the 8 m.y. old Siwalik species "*Cormohipparion*" (*Sivalhippus*) *perimense* (sensu Bernor and Hussain, 1985; "*Sivalhippus*" *perimense* of Bernor et al., in press), sharing all the characters cited above except that it has retained a small, anteriorly placed preorbital fossa.

"*Cormohipparion*" (*Sivalhippus*) *perimense* shares plesiomorphically with "*Hipparion*" *houfenense* the lack of any strong nasal retraction. However, the two share the derived character of a strongly developed, persistent protostylid on all mandibular cheek teeth except p2. *Proboscidipparion sinense* has relatively weak and nonpersistent protostylids which may have been lost convergently with most other hipparionine lineages.

If the phylogenetic hypothesis of Flynn and Bernor (1987) and Bernor et al. (in press) for these taxa is correct, it would falsify Zhegallo's (1978) hypothesis that "*Hipparion*" *houfenense* is directly derived, via migration, from the North American genus *Neohipparion.* Interestingly enough, the proposals made by Flynn and Bernor (1987) and Bernor et al. (in press), as well as those in this paper, correspond most closely with Gromova's (1952) suggestion that *P. sinense* and "*Hipparion*" *houfenense* are evolutionarily related. Bernor et al. (in press) have provisionally chosen to retain Sefve's (1927) genus designation *Proboscidipparion,* assigning both *P. sinense* and *P. pater* to it, but recognizing that this genus belongs to a radicle of predominantly southern and eastern Asian and African late Miocene-Pleistocene hipparions they refer to the "*Sivalhippus*" Complex. Resolution of this superspecific group's explicit phylogenetic relationships and taxonomic ranking awaits further study and analysis.

"*Hipparion plocodus*"
Sefve, 1927

Hipparion plocodus Sefve, 1927: 18–20, pl. 3, fig. 11.

REMARKS: Sefve (1927: 18–20; pl. 3, fig. 11) referred a palate fragment (PMU M3824; Locality 49) to *Hipparion plocodus.* Despite the fact that this specimen is fragmentary, Forsten (1985: 122) accepted it as lectotype for the species *Hipparion plocodus.* She also referred a vast assemblage of material from Localities 31, 43, 44, 49, 70, 73, Hsi Liang and Ch'iao–Chia Kou to this "taxon." The cheek teeth of PMU M3824 appear to have some apomorphic characters including very complex, thickly banded plications of the pre- and postfossettes, very complexly plicated pli caballins, and short and rounded protocones which primitively show some lingual flattening, particularly on the molars. Yet our experience is that in the absence of any other skull features such as the nasal notch, facial fossae, and preorbital bar, hipparion species can only rarely be confidently recognized. We prefer to regard "*Hipparion plocodus*" as a nomen dubium and discourage its further use.

Two other specimens in the PMU collection, M3825 and M348, show similarities to PMU M3824 in aspects of their cheek tooth morphology. PMU M3825 (Locality 43) is an adult male palate fragment with snout, right I1–2, left I1–3, both canines, and right and left P2–M3, but lacking the nasals, facial region, orbits, and cranium. The cheek teeth show a similar complexity of the pre- and postfossettes to M3824, and the protocones are similar in their morphology, although tend to be somewhat more oval shaped. PMU M348 (Locality 12) is an adult left palate fragment with the ventroposterior border of the preorbital fossa, left P2–M3 and right P2–M1 preserved. Complexity of the pre- and postfossettes and pli caballin is not as elaborate as in PMU M3824. The premolar protocones are rounded as in M3824, but the molar protocones show some slight elongation. There is little or no compelling reason to refer these specimens to any distinct species, although they do variably show some affinities with "*Hipparion plocodus.*"

"*Hipparion tylodus*"
Sefve, 1927

Hipparion tylodus Sefve, 1927: 43–45; fig. 23, p. 44; 93.

REMARKS: Sefve (1927: 43–45; text fig. 23, p. 44; 93) erected the species *Hipparion tylodus* for PMU M3864, an adult male individual, from Locality 73. This specimen appears to have been broken during field collection, along a horizontal plane at the midorbital level. What remains are the snout, right and left I1–3, C, P2–M3, and ventral portion of the orbits and anterior basicranium. The preorbital fossa, caninus fossa region, and nasal bones are missing. Only cheek tooth character states are preserved. The cheek teeth show complexly plicated pre- and postfossettes, bifid pli caballins (except P2 and M3 which are single), moderately to deeply incised hypoglyphs, and protocones which generally show rounding but still retain a lingually flattened or elongate aspect in some cheek teeth. The protocone, fossette, and pli caballin morphologies are remarkably similar to those of PMU M3824, "*Hipparion plocodus.*" The size and cheek tooth morphology are also similar to those of the other Locality 73 species, "*H.*" *ptychodus,* especially the very complex, thinly banded fossette plications. Given the incomplete state of preservation of this specimen, we recommend that "*Hipparion tylodus*" be regarded as a nomen dubium. Indeed, the original specimen may well be referable to "*H.*" *ptychodus.*

"*Hipparion parvum*"
Sefve, 1927

Hipparion parvum Sefve, 1927: 38–39.

REMARKS: Sefve (1927: 38–39, fig. 19) erected the species *Hipparion parvum* for a single broken palatal fragment (PMU M346) which included right P2–M3 and left M1–3. Sefve (1927: 38) reported that this specimen originated from Yu She Hsien, S10 Li, Tan Tsun, S20 Li, Ch'iao–Chia Kou. This specimen, which we infer to be the holotype by monotypy, is among the smallest in this collection, comparing most closely with "*H.*" *coelophyes* in size. PMU M346 also has a cheek tooth morphology similar to that of

"*Hipparion*" *coelophyes* in complex fossette plication, and preponderence of bifid pli caballins, moderately to deeply incised hypoglyphs, and consistently lingually flattened protocones. However, there is not enough of the specimen preserved to clearly distinguish it from other species. In fact, there is very little to preclude its referral to "*H.*" *coelophyes* (s.s.).

Hipparionine sp. indet.

Hipparion dermatorhinum Sefve, 1927 (in part): 17, text fig. 11.

REMARKS: As mentioned earlier, Sefve (1927: 17, fig. 11) referred a palate fragment (PMU M3823; Locality 43) to *Hipparion dermatorhinum.* This specimen has relatively complex, although thinly banded, plications of the pre- and postfossettes, the pli caballins are mostly single, hypoglyphs are variously shallow to deeply incised, and the protocones are lenticular shaped. While the lenticular-shaped protocones show similarities to those of the best preserved specimen of "*H.*" *dermatorhinum,* AMNH 41 L310, there is just too little critical morphological information to refer this specimen with any certainty to "*H.*" *dermatorhinum.*

CONCLUSIONS

Our study of the PMU collection of Chinese hipparionines, and referable AMNH specimens, has allowed a substantial revision of Sefve's (1927) original work on this collection. In our character state analysis we recognize 11 morphological groups noting the variability of 40 different discrete (mostly) character states.

As a result of this study, we recognize seven valid taxa in the Uppsala collection: "*Hipparion*" *platyodus, "Hipparion" coelophyes,* "*Hipparion*" *hippidiodus,* "*Hipparion*" *ptychodus,* "*Hipparion*" *dermatorhinum,* "*Hipparion*" *forstenae,* and *Proboscidipparion sinense.* We recommend that five taxa be regarded as nomina dubia because of the incompleteness of the original material described by Sefve (1927), or problems of subsequent taxonomic referral: "*Hipparion fossatum,*" "*Hipparion kreugeri,*" "*Hipparion plocodus,*" "*Hipparion*" *tylodus,* and "*Hipparion parvum.*" One incomplete specimen (PMU M3823) designated *Hipparion dermatorhinum* by Sefve (1927), is regarded here as hipparionine gen. and sp. indet.

While we have not made an explicit phylogenetic analysis of these taxa, we have cited some potential evolutionary relationships which we believe are suitable for future testing. We have argued that "*H.*" *platyodus,* "*H.*" *coelophyes* (s.l.), and "*H.*" *hippidiodus* form a morphological transformation series which may or may not represent an actual evolutionary relationship. Indeed, Bernor et al. (in press) have argued that "*Hipparion*" *platyodus* may be a primitive member of their "*Sivalhippus*" Complex, whereas we state here, in agreement with Qiu et al. (1987), that "*H.*" *hippidiodus* may be related to *Hipparion* s.s. "*Hipparion*" *ptychodus* is believed to be potentially related to the "*Sivalhippus*" Complex of Bernor et al. (in press), as potentially is *Proboscidipparion sinense.* "*Hipparion*" *forstenae* is a member of the *Hipparion* (*Cremohipparion*) lineage of Qiu et al. (1987; = Genus *Cremohipparion* of Bernor et al., in press), which includes several species ranging from the eastern Mediterranean to southwest Asia, the western U.S.S.R., and northern China. "*Hipparion*" *dermatorhinum* has been found to have a combination of plesiomorphic and autapomorphic features which have suggested to Bernor et al. (1988) that it may be a highly derived monospecific lineage restricted to Asia.

While the Uppsala collection of Chinese hipparionines is exceptional for its state of preservation, completeness of material, and species diversity, it does not contain all known species of Chinese hipparionines. Study of the IVPP and other contemporary Chinese collections by Qiu et al. (1987) and others (see section on Investigative History), as well as preliminary study of the AMNH collections by Bernor and Qiu, suggest that many more taxa are present in the Chinese Neogene. Their study, and eventual chronologic ordering, will have considerable scientific value for diverse paleobiological and geological studies.

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APPENDIX 1

Character State Distributions of Uppsala Chinese Hipparionine Skulls

Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
"*H.*" *platyodus* EA, 9.5–5 Ma																										
(1) PMU M3691	C	B	C	B	B	A	B	A	B	B	A	A	A	C	B	B	C	A	B	A		B/	B	C	B	A
(2) PMU M3685	D	B	C	B/	B	A	B	A	B	B	A	A	A		B	B	C		B			D	B	C	B	A
(3) AMNH 91 B979	C	B	B	C	C	A	B	B	B	B	A	A	A	C	B	B	C	B	B	A/	B	B/	B	C	B	A
(2) "*H.*" *coelophyes* EA, 8 Ma																										
(3) PMU M3688	C	B	D	C	C	A	C	B	B	B	A	A	A	C	B	B	C	B	B	A/	B	B	B	C	B	A
(4) PMU M3690	C	B	D	C	B	A	B	A/	B	B	A	A	A	D	B	B	C	A	B	A	B	B	B	C	B	A
(5) PMU M311	C	B	D	C	B	A	B	A	B	B	A	A	A	C	B	B	C	A	B	A	B	B/	B	C	B	A
(6) PMU M309	E	/	E	C	C	A	D	B		B	A	A	A		B	B	C	A/	B	A	B	B	B	C	B	A
(7) PMU M3689	E	B	F	D	D	A	D	B	B		A	A	A		B	B	C	A/	B	A/	B/	B	B	C	B	
(8) PMU M584	E	B	F	D	C/	A	D	B	B	B	A	A	A		B	B	C	B/	B	A	B/	C	B	C	B	A
(9) PMU M594															B	B	C	B	B	A	B	B/	B	C	B	
(10) PMU M590															B	B	C	B	B	A/	B	B/	B	C	B	A
"*H.*" *hippidiodus* EA, 8–6 Ma																										
(11) PMU M3819	F	B	G	D	D	A	D	B	B	B	A	A	A		B	B	C	C	B	B	C	C/	B	C	B	A
(12) PMU M249	F		G	D	D	A	D	B	B	B	A	A	A		B	B	C	B/	B	B	C	D	B	C	B	A
(13) PMU M596	E		G	D	D	A	D	B	B	B	A	A	A		B	B	C	C	B	B	B/	C/	B	C	B	
(14) PMU M595	E	B	G	D	D	A	D	B	B	B	A	A	A		B	B	C	B/	B	A/	B	C	B	C	B	
(15) PMU M247							D	B	B		A	A	A		B	B	C	B	B	B	D	C/	B	C	B	
(16) PMU M248															B	B	C	B	B	B	B/	C/	B	C	B	
(17) PMU M250																B	C	D	B	B	B	C/	B	C	B	
(18) PMU M3818															B	B	C	C	B	B/	C	C/	B	C	B	
(19) PMU M251																B	C	C	B	A	B	B/	B	C	B	
(20) PMU M252															B	B	C	D	B	B		D	B	C	B	A
(21) PMU M253															B	B	C	B	B	A	B	C/	B	C	B	
"*H.*" *ptychodus* EA, 8–4.5 Ma																										
(22) PMU M347	G	B	J	B	A	A	B	A	B	B	A	A	A		B	B	C	A+/	B	A	C	B	B	C	B	A
(23) PMU M3684		B	J	C	A	A	B	A	B	B	A	A	A	C	B	B	C	A+/	B	A	B/	B	B	C	B	A
(24) PMU M593	G	B	J	C	A	A	B	A	B	B	A	A	A		B	B	C	A	B	A	C	D	B	C	B	
(25) PMU M350	C	B	J	C	B	A	C	B	B	B	A	A	A		B	B	C	A	B	A/	A	C	B	C	B	A
"*H.*" *dermatorhinum* EA, 10–7.5 Ma																										
(26) PMU M3872	D	B	B	B	B	A	A	A	B	B	A	A	A	F	B	B	C		B	A	B	C/	B	C	B	
(27) PMU M260	D	B	B	B	B	A	A	A	B	B	A	A	A		B	B	C	B	B	A/	C	D	B	C	B	A
(28) PMU M259															B	B	C	A/	B	B/	A	B	B	C	B	A
(29) PMU M261															B	B	C	A/	B	A	A/	B	B	C	B	A
(30) AMNH 41 L310	D	B	B	B/	A	B	A	A	B	B	A	A	A	E	B	B	C	A	B	B	B	B/	B	C	B	A

APPENDIX 1—(*Continued*)

Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
"*H.*" *forstenae* EA, 9–7.5 Ma																										
(31) PMU M3873	B	B	B	C	C	A	C	B	B	B	A	B	A	D/	B	B	C				D	D	B	C	B	A
(32) PMU M269	B	B	B	C	C	A	C	B	B	B	A	B	A	D/	B	B	C		B							
(33) PMU M3820	B		B	C	C	A	C	B	B	B	A	B	A	E	B	B	C	B	B	A	B	C/	B	C	B	A
(34) PMU M267	B	B	B	C	C	A	C		B	B		B	A		B	B	C	B	B	A/	B	C/	B	C	B	A
(35) PMU M268	B	B	B	C	C	A	C	B	B	B			A		B	B	C	B	B	A/	B	D	B	C	B	A
(36) PMU M585	B	B	B	C					B	B	A	B	A		B	B	C	B	B	A/	B/	B/	B	C	B	A
(37) PMU M592	B	B	B	C	C	A	C	B	B	B			A		B	B	C						B	C	B	A
(38) PMU M591	B	B	B	C	C	A	C	A	B	B	A	B	A	D/		B	C		B	A/	C/	D	B	C	B	A
(39) PMU M586	B	B	B	C	C	A	C	B	B	B	A	B	A			B	C		B				B	C	B	
(40) PMU M7357	B	B	B	C	C	A	C	B	B	B	A	B	A			B	C		B				B	C	B	A
(41) PMU M7362	B	B	B	C	C	A	C	B				B	A													
(42) PMU M7359					C		C	B	B	B	A	B	A		B	B	C	A/	B	B	B/	B/	B	C	B	A
(43) 41 L352	B	B	B	C	C	A	?C	B	B	B	A	B	A	D	B	B	C	D	B	D	D	D	A/		B	A
(44) 41 L333	B	B	B	C	C	A	C	B	B	B	A	B	A	D	A/	B	C	B/	B	A	B/	B/	B	C	B	A
(45) 18 278	B	B	B	C	C	A	C	B	B	B	A	B	A	D	A/	B	C	C	B	A	B/	C/	B	C	B	A
(46) 19 L81	B	B	B	C	C	A	C	B	B	B	A	B	A	D	A/	B	C	C	B	B	B	B/	B	B	B	A
P. sinense EA, 3–2 Ma																										
(47) PMU M3925	H	B	G	E	D	A	E	B	B	B	A	A	A	H	B	B	D	A+	B	C	B	F	B	C	B	A
"*H. plocodus*"																										
(48) PMU M3824															B	B	C	A	B	A+/	B	B	B	C	B	A
(49) PMU M3825															B	B	C	A	B	A	B	B	B	C	B	A
(50) PMU M348															B	B	C	A/	B	A/	B/	C/	B	C	B	A
"*H. tylodus*"																										
(51) PMU M3864															B	B	C	A	B	A/	B/	B/	B	C	B	A
"*H. parvum*"																										
(52) PMU M346															B	B	C	A	B	A/	B/	B	B	C	B	A
Hipparionine sp. indet.																										
(53) PMU M3823															B	B	C	A/	B	A/	B/	G	B	C	B	A
(54) PMU M254																										
(55) PMU M588	B	B	B	C	B/	A	D	B	B	B	A	?	A	D	B	B	C	B/	B	B	A/	C/	B	C	B	A
(56) PMU M3821 A+B	B	D	C	B	A	C/	B	B	B	A	B	A		B	B	C	B	B		B/	D	B	C	B	A	
(57) PMU M7361																										

APPENDIX 1—(*Continued*)

Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
Additional Comparison Outgroup and Sister Taxa (after Bernor et al., in press)																										
P. leonensis NA, 19–18 Ma	A	?A	A	C	C	A	B/	B	A	A	A	A	A	A	A	A	A	D	A	D	B	D	A	A	?A	?A
M. insignis NA, 16–15 Ma	A	?A	A	C	B	A	A	A	A	A	A	A	A	A	A	A	A	C	A	B	A/	D	B	A/	B	A
C. goorisi NA, 15 Ma	B	A	C	A	A	A	B	A	B	B	A	A	A	A	A	?A	B	B/	A	B	B	D	B	B	?B	A
C. sphenodus NA, 14–12 Ma	B	A	B/	A	A	A	A	A	A/	B	A	A	A	A/	A	B	B/	B/	B	B	B	A	B	C	B	B
C. occidentale NA, 12–8 Ma	C	?B	B	A	A	A	A	A	B	B	A	A	A	C	B	B	C	B	B	A/	B	A	B	C	B	A
"*H.*" *primigenium* s.s., Eu, 11–8 Ma	C	B	B	A	A	A	A	A	B	B	A	A	A	C	B	B	C	A	B	A	B	B	B	C	B	A
"*H.*" *weihoense* EA, 11–10 Ma	C	B	B	A	A	A	A	A	B	B	A	A	A	C	B	B	C	A	B	A	B	B	B	C	B	A
"*S.*" *perimense* SA, 8 Ma	G	B	D	C	B	A	A	A	B	B	A	A	A	C	B	B	D	A	B	A	B	E	B	C	B	A
"*S.*" *houfenense* EA, 6–2.5 Ma	E	B	F	D	D	A	D	B	B	B	A	A	A	C	B	B	D	A	B	A	B	E	B	C	B	A
P. pater EA, 5–2 Ma	H	B	G	E	D	A	E	B	B	B	A	A	A	G	B	B	D	A+	B	A	B	B	B	C	B	A
C. moldavicum SWA, 9–8 Ma	B	B	C	B	A	A	A	A	B	B	A	A	A	C	B	B	C	B	B	A/	C	D	B	C	B	A

Legend—Taxa: *P. leonensis* (= *Parahippus leonensis*), *M. insignis* (= *Merychippus insignis*), *C. goorisi* (= *Cormohipparion goorisi*), *C. sphenodus* (= *Cormohipparion sphenodus*), *C. occidentale* (= *Cormohipparion occidentale*), "*H.*" *primigenium* s.s. (= "*Hipparion*" *primigenium* s.s.) "*H.*" *weihoense* (= "*Hipparion*" *weihoense*), "*S.*" *houfenense* (= "*Sivalhippus*" *houfenense*), "*S.*" aff. *houfenense* (= "*Sivalhippus*" aff. *houfenense*), *P. sinense* (= *Proboscidipparion sinense*), "*S.*" *perimense* (= "*Sivalhippus*" *perimense*), *C. moldavicum* (= *Cremohipparion moldavicum*).

NA = North America, Eu = Europe, SWA = Southwest Asia (includes Greek and Western U.S.S.R. localities), NAf = North Africa, EA = East Asia, SA = South Asia.

APPENDIX 2

Summary Character State Distributions of Uppsala Chinese Hipparionine Mandibles

Taxa	27	28	29	30	31	32	33	34	35	36	37	38	39	40
"*H.*" *platyodus* EA, 9.5–5 Ma														
(1) PMU M3691	A	A	A	C	C	C	C	A	B	B/	A	B	A	D
(3) AMNH 91 B979	A	A	A	A	A	C	A/	A	B	C	A/	B	A/	B
"*H.*" *dermatorhinum* EA, 10–7.5 Ma														
(30) AMNH 41 L310	A	A		A/	B	B/	B	A	B	B/	A/	B	A/	C
"*H.*" *forstenae* EA, 9–7.5 Ma														
(44) 41 L333	?	A	A	B		B		A		C	A	A	B	
P. sinense EA, 3–2 Ma														
(47) PMU M3925	A	A	A	C	C	C	C	A	B	C	B	B	D	D
Additional Comparison Outgroup and Sister Taxa (after Bernor et al., in press)														
C. goorisi NA, 15 Ma	A	A	A	A	A	A	A	A	B	B	B	B	A	A
C. sphenodus NA, 14–12 Ma	A	A		A	A	A	A	A	B	B	A	B	A	A
C. occidentale NA, 12–8 Ma	A	A	A	A	A	A	A	A	B	B	B	B	A	A/
"*H.*" *primigenium* s.s., Eu, 11–8 Ma	A	A	A	A	A	A	A	A	B	A/	A	B	A	B
"*S.*" *perimense* SA, 8 Ma	A	A	A	C	C	C	C	A	B	A	C	B	D	D
"*S.*" *houfenense* EA, 6–2.5 Ma	B	A	A	C	C	C	C	A	B	A	A	B	D	D
P. pater EA, 5–2 Ma	A	A	A	C	C	C	C	A	B			B	D	D
C. moldavicum SWA, 9–8 Ma	A	A	A	A	A	A	A	A	B	C	B	B	A/	B

Legend—same as Appendix 1.

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